REVUE SUISSE DE ZOOLOGIE, 102 (2) : 425-474; juin 1995

Phylogeny of Scaphidiinae with redefinition of tribal and generic limits (Coleoptera: Staphylinidae)

Richard A.B. LESCHEN* & Ivan LÖBL**
*Snow Entomological Museum, Snow Hall, University of Kansas, Lawrence, Kansas, 66045, USA.
**Muséum d'histoire naturelle, Case postale 6434, CH-1211, Geneve 6, Switzerland.

Phylogeny of Scaphidiinae with redefinition of tribal and generic limits (Coleoptera: Staphylinidae). - The phylogenetic relationships among the higher categories of the Scaphidiinae and genera of the Cypariini, Scaphiini and Scaphidiini are investigated using cladistic analysis. Terminal taxa examined include all genera of these higher taxa except for the Scaphisomatini (including the Heteroscaphini and Toxidiini) for which we examine exemplars. A total of 69 characters (including 3 multistate characters) are enumerated for cladistic analysis. Members of the Apateticinae, Piestinae, and Trigonurinae are used to polarize characters. Two cladograms are produced from the analyses: Cypariina (Scaphiina (Scaphisomatini + Scaphidiina)) and ((Cypariina + Scaphidiina) (Scaphisomatini + Scaphidiina)). On the basis of these cladograms we elevate the subtribes Scaphidiina and Scaphiina to tribal level and eliminate the subtribes Diateliina and Cerambyciscaphina. The following generic level synonymies are made: *Episcaphium* (=*Phenoscaphium*), *Scaphidium* (=*Ascaphidium*, *Cribroscaphium*, *Hemiscaphium*, *Falsoascaphidium*, *Scaphidiolum*, *Scaphidopsis*). We review the genera of the Cypariini, Scaphiini and Scaphidiini and provide a catalogue for the described species that includes new combinations resulting from proposed generic synonymies. A replacement name, *Scaphidium pauliani*, is proposed for *Scaphidium sulcatum* Paulian. Information on biology, distribution, and larval descriptions is reviewed for each genus.

Key-words: Coleoptera - Staphylinidae - Scaphidiinae - taxonomy - phylogeny - mycophagy.

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* Present address: Department of Entomology, Michigan State University, East Lansing, Michigan, 48824-1115, USA.

Manuscript accepted 09.01.1995.

INTRODUCTION

The staphylinid subfamily Scaphidiinae is a taxonomically diverse group of beetles with about 1300 species worldwide (Löbl, 1992). Most scaphidiine species occur in tropical and subtropical regions with the highest number of described species in southeast Asia; however, the scaphidiine fauna is virtually undescribed in most other tropical regions. The large number of specimens available in museum collections collected by flight-intercept traps, leaf-litter sifting, and canopy fogging indicates that many undescribed species are being discovered regularly.

Scaphidiines are among the most speciose groups of beetles that are strictly mycophagous. Adults may occur on a variety of fungal taxa while oviposition and larval development may be more specialized (Newton, 1984). For example, among specialists, some species of *Baeocera* and *Scaphobaeocera* (Scaphisomatini) feed exclusively on the spores of myxomycetes (Lawrence & Newton, 1980; Newton, 1984; Newton & Stephenson, 1990; Newton, 1991), and species of *Scaphium* and *Cyparium* usually feed on the fruiting bodies of Agaricales and other fleshy Basidiomycetes (Ashe, 1982; Newton, 1984; Kompantsev & Pototskaya, 1987). Because of their fungal host patterns, scaphidiines are an attractive group to be studied for patterns of mycophagy from both ecological and phylogenetic perspectives.

Most of the species of Scaphidiinae are small (1.0-3.0 mm) and black or reddish-brown in colour; however, some groups of genera have species that may be larger (11 mm or more) with striking colour patterns. Many species of scaphidiines exhibit male secondary sexual characteristics besides dilated protarsomeres (and sometimes the mesotarsomeres) that occur in many groups of staphylinoids. For example, both sexes of *Diatelium wallacei* (Fig. 1) have extremely long necks; however, only some male specimens have necks that attain lengths greater than the lengths of their bodies. All male specimens of the subtribe Scaphidiina have well-developed setiferous patches on their metasterna. The setae are curled at their ends and at the base of each seta there are 2-3 small pores (Figs 18,19); usually setae occurring on other parts of the body have only a single associated pore. The setiferous patches appear to be similar to sex patches of male beetles described by Faustini & Halstead (1982). Males of *Scaphidium* and *Euscaphidium* have stridulatory files on the prescutum that articulate with corresponding plectra on the inner posterior margin of the pronotum (Figs 17, 32). The numbers of files vary from 7 to 11. Curiously, the pronota of males in some of these species have a large median hump that may be related to the function of the scutellary file.

The first scaphidiine species was described in 1758 by Linné and suprageneric rank was given to the group by Latreille (1807). Since LeConte & Horn (1883), the scaphidiines were treated as a family and usually placed close to the staphylinids. Casey (1893) distinguished two groups among the Scaphidiidae: the Scaphidiini and the Scaphisomatini (incorrectly spelled as Scaphisomini). Subsequently, Achard (1914) and Pic (1915b) erected the tribes Cerambyciscaphini and Heteroscaphini, respectively. Achard (1924) proposed a new classification for the 41 genera that he recognized. Many characters on which his tribes and subtribes were based are variable

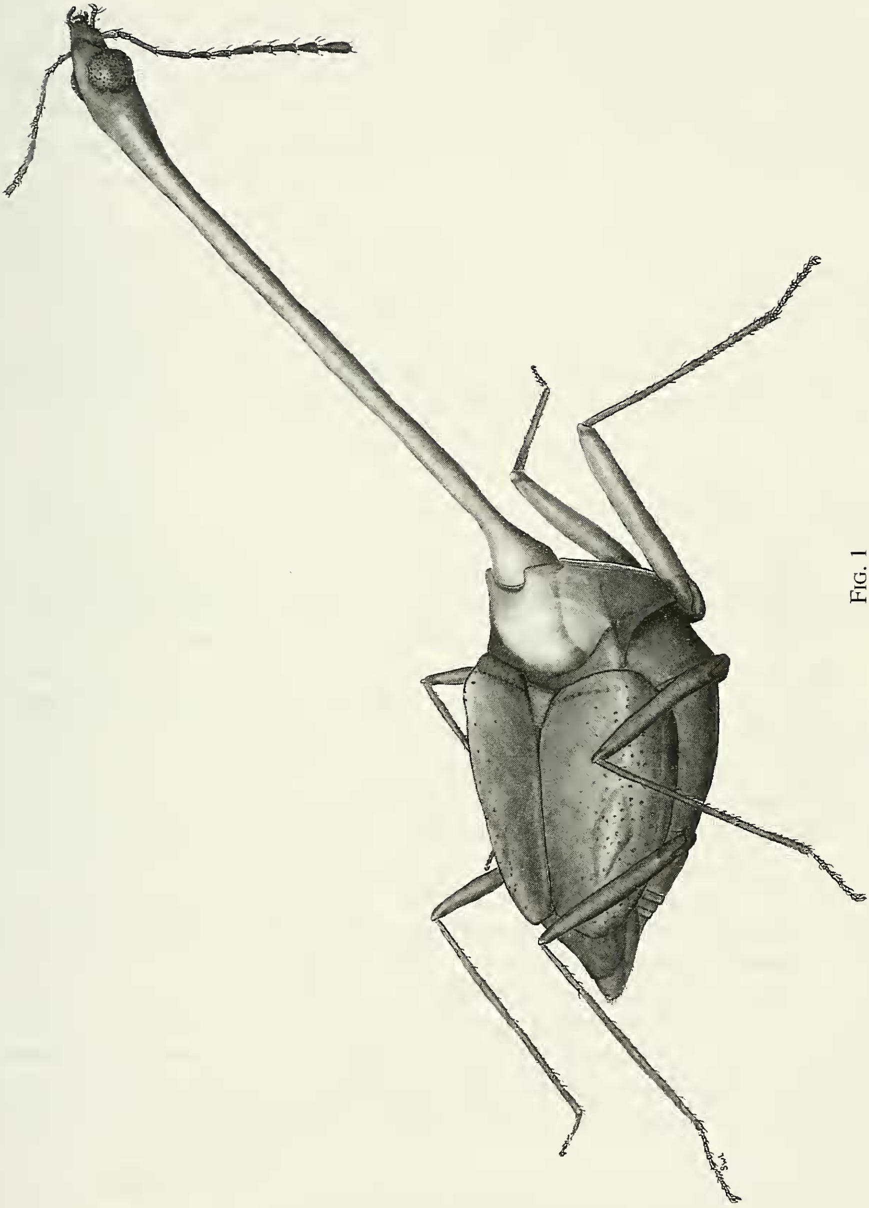


FIG. 1

Habitus of *Diatelium wallacei*, lateral view.

and inconsistent among the higher categories. Achard's classification was essentially ignored by subsequent workers. KASULE (1966), in a study of the larvae of British Staphylinoidea, recognized that scaphidiid larvae share many characteristics with some members of the Staphylinidae and changed the status of the family to subfamily, placing the group near the Euaesthetinae and Oxyporinae. Perhaps ignorant of Kasule's work, TAMANINI (1969) separated the Scaphidiidae into two families, the Scaphidiidae and Scaphisomidae, based mainly upon characters of the prosternum and antennae. Recognizing natural affinities as Kasule did, LAWRENCE & NEWTON (1982) placed the scaphidiids in their "oxyteline group" of Staphylinidae, and currently LAWRENCE (1991) and NEWTON & THAYER (1992) treat the scaphidiids as a subfamily. The current classification is shown in Table 1.

To date no classification has been proposed for the Scaphidiinae based on a sound phylogenetic analysis, and the classification of the Scaphidiinae has essentially remained unchanged since ACHARD (1924) with modifications of family-group names (NEWTON & THAYER, 1992). In the present study the phylogenetic relationships of the higher categories will be studied, the genera that have been placed in the tribes Scaphidiini and Cypariini are reviewed, and a catalogue for the included species (Appendix) is provided.

MATERIALS AND METHODS

Examinations of characters are made from pinned, glycerin-dissected, and slide-mounted adult specimens. First, beetle specimens are placed in cold KOH (10% solution) until the internal tissues are macerated. Further clearing of the cuticle in hydrogen peroxide is necessary for some specimens. After rinsing in water, specimens are placed into glycerin (for glycerin-dissections) or into serial solutions of water:alcohol (until water is removed) for slide-mount preparations. The cleared beetle is placed into a drop of Euparal (Chroma-Gesellschaft, Kongen/Necker) on a microslide and the dissection performed using fine dissecting needles. Once the beetle is dissarticulated and the parts properly arranged, the dissection is dried for two hours until the dissected parts are stationary. To prevent crushing of larger specimens, cover-slip props are inserted into the Euparal. The dissection is placed on a slide drier for 24 hours, then additional layers of Euparal are added to the specimen and the cover-slip applied. Thorough drying requires about two weeks. Pinned specimens are examined for external characters. Internal characters in rare taxa are examined in specimens that are softened in water. Dissection of genitalia from pinned specimens follows that of LESCHEN & *al.* (1989). Specimens examined are deposited in the Muséum d'histoire naturelle, Geneva, Muséum National d'Histoire Naturelle, Paris, Museo Civico di Storia Naturali, Genova, Snow Entomological Museum, University of Kansas, Lawrence, and the R. Leschen collection.

Terminology for some external structures we use is described in LESCHEN & *al.* (1989). Lengths of beetles are measured from the apex of the head to the tip of the elytra.

Terminal taxa for the phylogenetic analysis include all genera of the Cypariini and Scaphidiini. Several generic level synonymies that we establish within the Scaphidiinae are based on unique and unreversed synapomorphies (see taxonomic sections for details). Also, ACHARD (1924) recognized the Heteroscaphini and Toxidiini as separate tribes from the remaining Scaphidiinae. On the basis of unique and unreversed characters (procoxal cavity, see character 25; mesosternal process anvil-shaped, filiform antennomeres) we believe that the Scaphisomatini, Heteroscaphini, and Toxidiini, should be grouped together and that the two latter taxa should be included as subtribes in the Scaphisomatini. Monophyly of each of the subtribes in the Scaphisomatini is questionable. Species examined among the Cypariini, Scaphidiina, and Scaphiina are indicated in the species catalogue (Appendix). Members of the following Scaphisomatini are examined: *Baeoceridium* Reitter, *Vituratella* Reitter, *Scaphisoma* Leach, *Baeocera* Erichson, *Scaphobaeocera* Csiki, *Toxidium* LeConte, *Bironium* Csiki, *Pseudobironium* Pic, and *Birocera* Löbl.

Determinations of character state polarities are based on outgroup comparisons to the subfamilies Apateticinae (*Apatetica princeps* Sharp and *Nodynus leucofasciatus* Lewis), Piestinae (*Siagonium* spp. and *Zirophorus* spp.), and Trigonurinae (*Trigonurus asiaticus* Reiche) which together with the Scaphidiinae are members of the oxyteline group of staphylinids (LAWRENCE & NEWTON, 1982). Scaphidiines most closely resemble members of the Apateticinae based on the form of the elytra that cover abdominal tergites 1 and 2 and the form of the abdomen that is abruptly narrowed posteriorly and not parallel-sided (like most members of the Oxyteline group). Until there is a phylogenetic hypothesis of the higher taxa of the oxyteline group, the definitive sister relationship of the Scaphidiinae is unknown.

Characters enumerated for phylogenetic analysis from adult specimens are hypothesized to be homologous. Details regarding determination and evaluation of characters, their states, and polarities are discussed in the section on character analysis. Data are binary coded and entered into MacClade version 3 (MADDISON & MADDISON, 1992). Numbers for characters correspond to those in the data matrix, character analysis, and cladograms. Characters are mapped onto cladograms using ACCTRAN optimization (MADDISON & *al.*, 1984).

Because the relationships among the outgroup taxa, and the remaining members of the oxyteline group are unknown, we perform separate analyses using different specifications for outgroup taxa. One analysis is based upon the inclusion of all three members of the outgroups, Piestinae, Trigonurinae, and Apateticinae, as terminal outgroup taxa (we specify that these form a monophyletic group). In the other analysis a generalized outgroup is constructed from the three taxa; and, any polymorphism among the outgroup is coded in the data matrix entered into MacClade. When different outgroup taxa are used in the phylogenetic analysis, polarities of characters should change resulting in different tree toplogies.

Phylogenetic analyses are performed with PAUP 3.1.1 (Swofford, 1993) and character analysis assisted with MacClade. All multistate characters are treated as unordered and all characters are assigned equal weight in PAUP. We used the heuristic tree search option for generating cladograms with the following options: branch swapping on all starting trees (even non-minimal trees), branch swapping with steepest descent, and the addition sequence random. Alternative branching patterns were examined with MacClade.

At the beginning of this study it was not clear to us that *Kathetopodion borneense* (Pic) was a member of the Scaphisomatini. Two features of this species are similar to those of the outgroups; the tarsomeres are relatively thick (not thin and elongate as they are in members of the Scaphisomatini) and the head is somewhat prognathous. We decided to include *K. borneense* as a terminal taxon and allow the parsimony analysis to determine the placement of the species.

CHARACTER ANALYSIS

Characters used for reconstructing the phylogeny of the Scaphidiinae are listed below and each description indicates how polarities have been interpreted for each character. The number of each character corresponds to the characters as they appear in the data matrix (Table 3) and the cladogram (Fig. 40). The number in parentheses indicates how each state is coded in transformation series for each character. Plesiomorphies appear first followed by apomorphies.

For many of the characters it is necessary to have adequate dissections for observation. Because there is a lack of specimens for some scaphidiines, species could not be dissected entirely; and these include the following: *Euscaphidium tuberosum* Achard (2 males), *Cerambyciscapha dohertyi* Pic (1 male), and *Kathetopodion borneense* (Pic) (2 females).

1. HYPOPHARYNGEAL SETAE (Figs 20, 21, 30). (0) Arranged into a peripheral comb of evenly spaced setae surrounding the hypopharynx; (1) without peripheral comb of setae. All members of the ingroup have scattered setae on the hypopharynx but lack the distinct setal comb present in most species of Staphylinidae. The distribution of the setae among the ingroup taxa varies. The setae are scattered on the entire surface of the hypopharynx (*Scaphium*) or confined to lateral portions (other taxa examined). The hypopharyngeal setae may be elongate (*Scaphium*) or short (Scaphisomatini) or composed of different sizes (in some members of the Scaphidiina). The variation of the hypopharyngeal setae appears to be species specific and may not be appropriate for higher level analyses. Character state (1) does not occur in the outgroup and it is therefore inferred to be apomorphic.

2. GALEAL SETAE (Figs 26, 27). (0) Elongate and not bristle-like; (1) short and bristle-like. All members of the ingroup have setae that are shortened, and arranged into distinct rows. Among the outgroup taxa, the setae are elongate and either arranged into rows (members of the Piestinae and Trigonurinae) or not (members of the Apateticinae). The setae on the galea of members of the Scaphidiinae are bent, or slightly bent, and spatulate at their apices. Character state (1) does not occur in the outgroup and it is, therefore, inferred as apomorphic.

3. SHAPE OF THE LACINIA (Figs 26, 27) (0) Broadly flattened with a well-developed hyaline inner margin; (1) not especially flattened with a poorly developed hyaline inner margin. Among members of the outgroup the lacinia is a broad appendage that has a large hyaline margin that bears setae along its inner edge. In contrast, most members of the Scaphidiinae have a comparatively narrower lacinia with a reduced hyaline region that bares elongate setae at its apical and subapical margins. In *Kathetopodion* the lacinia is flattened and hyaline and is similar to that observed in the outgroup. Character state (1) is absent from the outgroup and it is, therefore, inferred to be apomorphic.

4. APEX OF THE MANDIBLE (Figs 22, 24). (0) With one incisor lobe; (1) with two teeth. Among members of the Scaphidiini and *Cyparium*, and some members of the Scaphisomatini, the mandible has two apical teeth and in other members of the Scaphisomatini there are taxa that have a simple or bifid apex. In the latter taxon this character is coded as polymorphic. Among members of the outgroup, the Piestinae have two or three teeth, and these are located at the margins of the mandible. It is not clear as to whether or not the lateral teeth in Piestinae are homologous to the subapical teeth in Scaphidiinae. The mandibles of Piestinae are not as dorsoventrally flattened and their lateral teeth are more strongly produced than those of Scaphidiinae. Although unlikely, it is possible that scaphidiine subapical teeth are derived from lateral teeth present in an ancestor and they have subsequently moved to a distal position. Until outgroup relationships are resolved and variation among oxyteline group members is investigated, the polarity of this character is equivocal.

5. SUBAPICAL SERRATIONS ON THE INCISING MARGIN OF THE RIGHT MANDIBLE. (0) Absent; (1) present. Except for *Kathetopodion*, all specimens examined of the ingroup have a serrate margin on the subapical edge of the mandible. Members of the outgroup do not have the serrate margin and, therefore, character state (1) is inferred as apomorphic.

6. SETAE ON THE ANTERIOR MARGIN OF THE LABRUM (Figs 23, 25). (0) Frayed; (1) bifid. Among members of the oxyteline group, the setae along the margin of the labrum may be simple or modified in forms that are apically frayed, branched, or barbed along the shafts. Among the ingroup, *Kathetopodion* and the Scaphidiina have labral setae that are relatively short and apically bifid, the setae are somewhat frayed in the Scaphiina, and among members of the Scaphisomatini there are short setae that are either simple or apically bifid (this character is coded as polymorphic for the Scaphisomatini). Character state (1), present among the ingroup, is inferred as apomorphic.

7. SHAPE OF LABRUM (Figs 23, 25). (0) Deeply emarginate; (1) not deeply emarginate. Among members of the outgroup, the labrum is deeply incised and somewhat v-shaped. In contrast, among members of the ingroup the labrum is slightly emarginate. Character state (1) is absent in the outgroup, and it is, therefore, inferred as apomorphic.

8. EPIPHARYNX (Figs 23, 25). (0) With peg-like sensilla; (1) without peg-like sensilla. All members of the ingroup, with the exception of *Cerambyciscapha*, and the Piestinae have campaniform sensilla present at the surface of the epipharynx. Members of *Trigonurus*, Apateticinae, and *Cerambyciscapha* have peg-like sensilla at the surface of the epipharynx. Until phylogenetic relationships among the outgroup are known, polarity of this character is uncertain.

9. SHAPE OF ANTENNAL CLUB IN CROSS-SECTIONAL VIEW (Fig. 14). (0) Round; (1) slightly flattened, (2) completely flattened. Among members of the outgroup, the antennomeres are rounded in cross-section, and are typically 2 times longer than wide. Among the ingroup taxa there are two additional states associated with the form of the anntennal club; the antennomeres are slightly flattened and compressed (1) or the antennomeres are completely flattened (2). Among scaphisomatines, some taxa (such as *Bironium*) have elongate antennomeres (many times longer than wide) that are filiform and rounded in cross section. This character is coded as polymorphic for the Scaphisomatini. Character states (1) and (2) do not occur in the outgroups, and, therefore, these are inferred as apomorphic.

10. ANTENNOMERES 3 - 11. (0) Symmetrical; (1) asymmetrical. All members of the outgroup have antennomeres that are symmetrical. Among the ingroup taxa, only some members of the Scaphisomatini and *Kathetopodion* have antennomeres that are asymmetrical in shape. In other scaphisomatines, such as *Bironium*, the antennomeres are not flattened or asymmetrical, and this character is coded as polymorphic for this tribe. Character state (1) does not occur in the outgroup and it is, therefore, inferred as apomorphic.

11. ANTENNOMERE 8. (0) Equal in size to antennomeres 7 and 9; (1) reduced, smaller than antennomeres 7 and 9. Antennomere 8 is equal in size and proportion to other antennomeres forming the club among members of the outgroup, the Scaphidiini and *Cyparium*. Antennomere 8 is reduced in *Kathetopodion* and most members of the Scaphisomatini (antennomere 8 is equal in length to 7 and 9 in specimens of *Bironium*). This character is coded as polymorphic for the Scaphisomatini. Character state (1) does not occur in the outgroup and it is, therefore, considered to be apomorphic.

12. ANTENNAL INSERTION. (0) Hidden below the frons; (1) visible. Among members of the outgroup, the frons is well-developed, concealing the antennal insertions in dorsal view. In all members of the scaphidiines the frons is highly reduced such that the antennal insertions are visible in dorsal view. Character state (1) is absent in the outgroup and it is, therefore, inferred as apomorphic.

13. EYE. (0) Entire; (1) notched. Among members of the outgroup, the eye is entire (0). In the scaphidiines, the eye may be notched at the antennal insertion. This condition is variable in members of the Scaphisomatini. The eye is entire in members of *Scaphium*, *Cyparium*, *Kathetopodion*, and some members of the Scaphisomatini. The character is coded as polymorphic for the Scaphisomatini. Character state (1) is absent in the outgroup and it is, therefore, considered as apomorphic.

14. TEMPORAL REGION OF THE HEAD (Figs 1, 2, 3). (0) Extending posteriorly a length as long as that of the eye, a neck is present; (1) less then 1/4 the width of the eye, a neck is absent; (2) at least 3 times the length of the eye. A distinct temporal region that is constricted behind the eyes and inserts into the prothorax is present among all members of the outgroup. This condition is also present in members of the Scaphiina; but, a distinct tempora is absent among the remaining members of the scaphidiines. Unique among staphylinoids, the unusually long neck of the species *Diatelium wallacei* Pascoe (character state (2)) is typically longer than the prothorax. Character states (1) and (2) are found among members of the ingroup and character state (0), present in the outgroup, suggests character states (1) and (2) are apomorphic.

15. GULAR SUTURES (Figs 2, 3). (0) Separate; (1) fused. The gular sutures at the base of the head are separated and form a distinct gula in members of the Trigonurinae, Apateticinae, and *Siagonium* (Fig. 2). The gular sutures are fused in all members of the scaphidiines (Fig. 3). A specimen of *Zirophorus* appears to have contiguous gular sutures, although the endocarinae (which form part of the tentorium) remain separate. The Piestinae are coded as polymorphic for this character. The form of the gula is variable in staphylinids (EVANS, 1965), and the distribution of character states among the oxyteline groups is unknown. Polarity of this character is uncertain because of the variable distribution of character states in the outgroup.

16. ENDOCARINA AT BASE OF THE HEAD. (0) Present along entire length of the gular region of the head; (1) present along half of the length of the gular region of the head. Fusion of the gular sutures is associated with the development of a single endocarina at the floor of the head that forms part of the tentorium. Among members of the outgroup taxa that have a distinct gula, the endocarina is present along the floor of the head. Among members of the Scaphiina and some members of the Scaphisomatini this endocarina is present only in the basal half of the head. The character is coded as polymorphic in the Scaphisomatini. The endocarina is not visible (possibly absent) in the dissected specimen of *Diatelium* and we coded this character as (?) for this species. Character state (1) is not present in the outgroup and it is, therefore, inferred as apomorphic. This character is not observed in specimens of *Euscaphidium* and *Cerambyciscapha.*

17. SHAPE OF THE MENTUM. (0) Wider than long and rectangular; (1) about as long as wide and trapezoidal. The mentum occurs as a broad rectangular plate among members of the outgroup taxa. The mentum is reduced in size among members of the Scaphidiinae, and its length and width vary among members of the Scaphisomatini. The character state is coded as a polymorphism for the Scaphisomatini. Character state (1) is absent in the outgroup and it is, therefore, inferred as apomorphic. This character is not observed in the specimen of *Cerambyciscapha.*

18. POSTERIOR ANGLE OF THE PRONOTUM. (0) Rounded; (1) pointed. The posterior pronotal angle is rounded among members of the outgroup taxa. The shape of the posterior pronotal angle among ingroup taxa varies from rounded (among members of the

Scaphiina) to pointed (in members of the Scaphidiina). Both character states occur in members of *Episcaphium* and the Scaphisomatini: the character is coded as polymorphic in these taxa.

The general shape of the pronotum differs in the Scaphidiinae compared to the remaining members of the oxyteline group and other staphylinids. The pronotum in the scaphidiines is box-shaped with a large pronotal volume (HLAVAC 1975). Due to the form of the prothorax, the posterior angle, composed of the terminal juncture of the hypopleuron and the pronotum, meet at a more or less 90° angle. In contrast, the hypopleuron and the pronotum among other staphylinids either meet at a relatively low angle (Apateticinae) or, as in the case of Piestinae, a distinct posterior angle is absent and the pronotal margin has a complete bead that rests on the hypopleuron. The variation among prothorax types among outgroups cause difficulties in defining character states. When only the variation in the Scaphidiinae is considered: an angle that is pointed (character state 1) is defined by the presence of a posterior angle that is produced beyond the hind margin of the pronotum and there is a distinct angular termination. Because this condition is absent among members of the outgroup, character state (1) is inferred as apomorphic.

19. POSTERIOR ANGLE OF THE PROTHORAX MOLDED ONTO THE ANTERIOR ANGLE OF THE ELYTRON. (0) Absent; (1) present. The pronotal angle may be molded into a recess located at the anterior angle of the elytron. Members of *Episcaphium* and the Scaphisomatini are coded as polymorphic for this character. Character state (1), absent in members of the outgroup, is therefore considered as apomorphic.

20. BASAL TRANSVERSE STRIA ON THE PRONOTUM. (0) Absent; (1) present. A punctate stria at the basal portion of the pronotum is present in members of the Scaphidiini (absent in some species of *Scaphidium*), *Ascaphidium*, and *Episcaphium*. This stria is absent among the remaining members of the Scaphidiinae and the outgroup taxa. This character is coded as polymorphic for *Scaphidium*. Character state (1) is absent in the outgroup and it is, therefore, inferred as apomorphic.

21. PRONOTUM WITH MARGINAL BEAD. (0) Absent; (1) present. A distinct marginal bead on the pronotum is absent in members of *Trigonurus* and *Apatetica*. This character is coded as a polymorphism for Apateticinae. Determination of the polarity of these character states is uncertain because the phylogenetic relationships among members of the outgroup are unknown.

22. HYPOMERON. (0) Small; (1) large. Stated previously (see character 18) the pronotum of scaphidiines is unusual among the oxyteline group. An unusually large hypomeron, present in the Scaphidiinae, is one of several features associated with the modified prothorax (i.e., prothorax narrowed apically, high pronotal volume, posterior margin undulate, general reduction in the size of the prosternum (see character 23)). We code only the hypomeron as representative of the entire complex of characters. The presence of a relatively small hypomeron (0), present in the outgroup, suggests that a relatively large hypomeron (1), present in members of the Scaphidiinae, is apomorphic.

23. Prosternum in front of procoxae (Figs 4-6, 15, 31). (0) Well-developed, at least a length equal to 3/4 procoxal width; (1) reduced to a length less than that of coxae. Because the length of the prosternum in front of the procoxa is very variable among members of the scaphidiines and among the outgroup partitioning this character into several discret character states is difficult. Polarity of this character is also difficult without a phylogenetic hypothesis for the outgroup. Therefore, character coding is simplified to represent the extremes in the variation observed. Only the Scaphisomatini (Fig. 6) and *Cyparium* have a highly reduced prosternum in contrast to the remaining members of the Scaphidiinae and the outgroups that have a relatively larger prosternum. The presence of a large and distinct prosternum among members of the outgroup taxa suggests that character state (1) is apomorphic.

24. Procoxal cavity (Figs 4-6, 15, 31). (0) Partially closed behind; (1) completely open behind. The procoxal cavities among members of the outgroup taxa are partially closed behind by posterior flanges of the prosternum such that the proxocae do not contact the mesosternum. Among members of the Scaphidiinae, the procoxal cavities are not enclosed by the posterior flanges of the prosternum, and contact the mesosternum. Character state (1) is absent in the outgroup and is it therefore inferred as apomorphic.

25. Procoxal cavity (Figs 4-6, 15, 31) (0) Internally open; (1) internally closed by the prosternum; (2) internally closed by the fusion of the prosternum and hypomeron. The procoxae of scaphidiines are subtended by the prosternum, forming a broad internal bar or shelf supporting the coxaė (1). In Scaphisomatini the prosternum is fused with the hypomeron thereby forming complete internal closure of the procoxal cavity (2). Among members of the outgroup the procoxal cavity is completely open internally and, therefore, characters states (1) and (2) are inferred as apomorphic.

26. Keel on mesosternum (Figs 12, 13, 16). (0) Absent; (1) present. A well-developed keel on the midline of the mesosternum that inserts into the median space of the procoxae, is present among all members of the Scaphidiinae. Character state (1), absent among members of the outgroup, is inferred as apomorphic.

27. Transverse mesosternal ridge. (0) Absent; (1) present. A transverse ridge on the mesosternum, directly behind the keel, occurs in members of *Scaphium*, *Episcaphium*, and some species of *Scaphidium*. This character is coded as polymorphic for *Scaphidium*. Character state (1) is completely absent in the outgroup and it is, therefore, inferred as apomorphic.

28. Anvil-like process of the mesosternum. (0) Absent; (1) present. The members of the Scaphisomatini, including *Kathetopodion*, posses an anvil-like process on the mesosternal keel, which is absent in the remaining members of the Scaphidiinae and the outgroup. The process is variable: it may be diamond-shaped or triangulate in ventral view and is flattened on its ventral face where a small keel may be present. Character state (1) is absent in the outgroup and it is, therefore, inferred as apomorphic.

29. Width of mesosternal process (Figs 12, 13, 16). (0) Less than the width of mesocoxa; (1) equal to the width of mesocoxa; (2) more than width of mesocoxa. Among the outgroup taxa, the mesocoxae are approximate, separated by a relatively narrow mesosternal process. The width of the mesosternal process is equal to that of the mesocoxa in members of *Ascaphium*, some *Episcaphium*, *Scaphium*, *Kathetopodion* and other Scaphisomatini. The width of the mesosternal process exceeds that of the mesocoxa in the Scaphidiina, some members of the Scaphisomatini, and some members of *Episcaphium*. In the latter two groups, widths of the mesosternum are variable and the character is coded as a polymorphic for these taxa. Because the outgroup taxa have a narrow mesosternal process, character states (1) and (2) are inferred as apomorphic.

30. Process at anterior region of mesothorax. (0) Present; (1) absent. On the anterior portion of the mesothorax of members of the Scaphidiina there is a process that inserts into the lateral portion of the inner wall of the prothorax. This process is absent among the remaining members of the Scaphidiinae. The absence of character state (1) in the outgroup suggests that it is apomorphic.

31. Submesocoxal lines at middle of metasternum (Figs 12, 13, 16). (0) Not connected; (1) connected. Among members of the Apateticinae and Scaphidiinae there are submesocoxal lines that parallel the mesocoxal cavities that may end near the inner portion of the metasternum. These lines are connected at the middle of the metasternum among members of the Scaphiina (or not as in some *Episcaphium*), *Cyparium*, and some Scaphisomatini: this character is coded as polymorphic for the Scaphisomatini and *Episcaphium*. Although members of the Piestinae and Trigonurinae do not posess these lines, the presence of these in the scaphidiines and apateticines suggests that the lines may have been part of the groundplan of the Scaphidiinae. However, there is no phylogenetic information available for the outgroups, the Apateticines may not be sister taxa to the Scaphidiinae, and, therefore, polarity of this character is uncertain.

32. Submesocoxal lines Figs 12, 13, 16). (0) Without punctures; (1) with punctures. The submesocoxal lines bear punctures in most members of the Scaphidiinae, but punctures are absent in some members of the Scaphisomatini and in members of the Apateticinae. This character is coded as polymorphic for the Scaphisomatini. We infer that character state (1) is apomorphic because it is absent among members of the Apateticinae and submesocoxal lines are completely absent among the other members of the outgroup.

33. Longitudinal line in the midline of the metasternum (Figs 12, 18). (0) Absent; (1) present. This structure is observed in specimens that are either light in color or those that have been cleared for dissection. The longitudinal line is present only in members of the Scaphidiina. The absence of character state (1) in the outgroup suggests that it is apomorphic. This character is not observed in specimens of *Euscaphidium* and *Kathetopodion*.

34. Premetacoxal lines on metasternum. (0) Present; (1) absent. Premetacoxal lines are present in most members of the Scaphidiinae, but are absent in a few members of the Scaphisomatini. These lines are absent in specimens of *Trigonurus* and *Nodynus*. This character is coded as polymorphic for the Apateticinae and Scaphisomatini. The lines, present on the external portion of the metasternum, are associated with transverse endocarinae that articulate with the anterior portions of the metacoxae. Because of character variation and lack of phylogenetic resolution among the outgroup, determination of the polarity of this character is uncertain.

35. Metasternal process (Figs 13, 16). (0) Absent; (1) present. Among members of the Scaphiina, *Cyparium*, some Scaphisomatini, and some species of *Scaphidium* there is a distinct metasternal process separating the metacoxae. This process is often delimited anteriorly by a visible thin line, or when cleared, is delimited by an endocarina visible through the cuticle where its edge is part of an endocarina that serves as part of an attachment site for the metendosternite. Sometimes the metasternal process bears smaller terminal processes (often present in males of some species) and it may be divided by a thin line along its midline. This character is coded as polymorphic for the Scaphisomatini and *Scaphidium*. Members of the outgroup lack character state (1) and it is, therefore, inferred as apomorphic.

36. Metasternum with only one macroseta per side (Figs 13, 16). (0) Absent, or with more than 1 seta per side; (1) present. The metasternum bears one seta per side among members of *Cyparium*, Scaphiina, and Scaphisomatini. In one specimen of *Episcaphium* there are two setae on one side of the metasternum. This character is variable in *Episcaphium* and Scaphisomatini and these are coded as polymorphic for this character. Among members of the outgroup, the Apateticinae and *Trigonurus* completely lack the macrosetae, in contrast there are 2 macrosetae per side in *Siagonium* and 4 per side in *Zirophorus*. Determining the groundplan for this character is problematic because the numbers of macrosetae vary in the outgroup and there is a lack of phylogenetic information for the outgroup relationships.

37. Metasternum of male with setiferous sex patch (Figs 13, 16, 18, 19). (0) Absent; (1) present. The metasternum of male specimens of the Scaphidiina posess a patch of closely packed setae that are curled at their ends. Males of some members of Scaphisomatini (such as some species of *Baeocera*) have macrosetae, but differ from those in the Scaphidiina in that these are not closely packed and do not have curled ends. The different appearance of the setiferous male patches among the Scaphidiina and Scaphisomatini suggests that this character is homoplastic. Male specimens of members of the outgroup taxa do not have character state (1) and it is, therefore, inferred as apomorphic. Male specimens of *Kathetopodion* are unknown.

38. Metacoxae. (0) Approximate; (1) separate. The metacoxae among the members of the outgroup taxa are approximate, separated by a narrow intercoxal process arising from the first visible abdominal sternite. Among all members of the scaphidiines, with

exception of those taxa that are laterally compressed in the Scaphisomatini (e.g., *Scaphobaeocera* and *Toxidium*), the metacoxae are separate and there is a relatively broad intercoxal process. This character is coded as polymorphic for the Scaphisomatini. Character state (1) is absent in the outgroup taxa and it is, therefore, inferred as apomorphic.

39. ANTERIOR ARMS OF THE METENDOSTERNITE (Figs 10, 33). (0) Present; (1) absent. The anterior arms of the metendosternite among members of the outgroup taxa are well-developed (Fig. 33); in contrast, all members of the scaphidiines completely lack the anterior tendons. In scaphidiines the anterior tendons may have moved into a terminal position where the apices of the furcal arms are somewhat expanded or frayed. Another feature of the metendosternite that appears to be tightly coupled with the reduction of the frontal arms is a shortening of the median stalk. Because both of these characters covary, we do not treat a shortened stalk as a separate character. Reduction of the anterior tendons (1) does not occur in members of the outgroup and are considered as apomorphic. This character is not observed in specimens of *Euscaphidium*, *Cerambyciscapha*, and *Kathetopodion*.

40. MEDIAN CARINA ON THE STALK OF THE METENDOSTERNITE (Figs 10, 33, 34). (0) Absent; (1) present. A median carina is present on the stalk of the metendosternite in members of the Scaphiina, *Cyparium*, and some Scaphisomatini. This character is also present in a dissected specimen of *Zirophorus*. This character state is coded as polymorphic for the Piestinae and Scaphisomatini. Character state polarity for this character is uncertain because of the lack knowledge about the phylogenetic relationships of and variation of the metendosternite among members of the outgroup. This character is not observed in specimens of *Euscaphidium*, *Cerambyciscapha*, and *Kathetopodion*.

41. STRIDULATORY FILE ON THE PRESCUTUM OF THE MALE (Fig. 17). (0) Absent; (1) present. A stridulatory file is present on the prescutum of male specimens among members of the Scaphidiina. Character state (1) is absent among members of the outgroup and it is, therefore, inferred as apomorphic. Male specimens are unknown for *Kathetopodion*.

42. VISIBLE PORTION OF SCUTELLUM. (0) Almost as large as entire mesonotum; (1) 1/2 to 1/4 as large as entire mesonotum. The size of the scutellum is relatively large in relation to that of the entire mesonotum among members of the outgroup; in contrast, it is relatively small among members of the Scaphidiinae. Among some members of the Scaphisomatini, the scutellum may be reduced to a size barely visible at the base of the elytra or completely absent. The absence of character state (1) in the outgroup suggests that it is apomorphic.

43. EPIPLEURON IN LATERAL VIEW. (0) Oblique; (1) almost vertical. The relative angle of the epipleuron in relation to the horizontal plane of the body is oblique among members of the Apateticinae, *Trigonurus*, *Cyparium*, *Kathetopodion*, and some members of the

Scaphisomatini. The epipleuron is relatively vertical in members of the Piestinae, some members of the Scaphisomatini and Scaphidiini. This character is coded as polymorphic for the Scaphisomatini. Polarity of this character is uncertain because of the lack of information regarding phylogenetic relationships and variable distribution of character states among members of the outgroup.

44. POSTERIOR MARGIN OF THE ELYTRON. (0) Without serrations; (1) with serrations. The posterior edge of the elytron in members of the Scaphidiinae typically has a serrate margin composed of widely spaced teeth that are directed laterally, away from the midline. The teeth may line the posterior edge to the inner flange of the elytron: the teeth are more spine-like at the inner flange of the elytron. Most members of the Scaphidiinae have a serrate edge, but it is absent in some species of Scaphisomatini and *Scaphium*; for these taxa this character is coded as polymorphic. Among members of the outgroup, similar structures occur in species of the Piestinae. In contrast to the regularly spaced teeth of the Scaphidiinae, the teeth on the posterior edge of the elytron in the observed Piestinae are irregular and are directed posteriorly, suggesting that the condition in the Piestinae may not be homologous to that found in Scaphidiinae. Polarity of this character is uncertain because of the lack of information regarding phylogenetic relationships of and variable distribution of character states among members of the outgroup.

45. INTERLOCKING TEETH ON THE INNER MARGIN OF THE ELYTRON. (0) Absent; (1) present. Among members of the Scaphidiina and Scaphisomatini there is an elytral interlocking mechanism at the inner sutural margins of the basal part of the elytra. It consists of a series of small teeth that fit into corresponding sockets. Among members of the Scaphidiina the teeth are undulate and smooth-sided, in contrast, those of the Scaphisomatini are jagged and pointed. On the basis of their different microstructure this character may be homoplastic. Character state (1) is absent among members of the outgroup and it is, therefore, inferred as apomorphic. This character is not observed in specimens of *Euscaphidium*, *Cerambyciscapha*, and *Kathetopodion*.

46. ABDOMINAL SPIRACLES 1 to 3. (0) In sclerotized region of the terga; (1) in membranous region of the terga. Like other members of the Staphylinidae, there has been extensive modification of the abdomen, especially in the reduction and fusion of the number of tergal elements. Among members of the Scaphidiinae there is a general reduction in the number of paratergites (see characters 48-52): they are no longer sclerotized and it is difficult to distinguish them from adjacent intersegmental membranes. Among members of the Scaphidiinae, abdominal spiracles 1-3 (or 1-2 in *Cyparium*) are consistently in a membrane while spiracles 1-3 among members of the outgroup are all contained within sclerotized paratergites. Character state (1) is absent in the outgroup taxa and it is, therefore, inferred as apomorphic. This character is not observed in specimens *Euscaphidium*, *Cerambyciscapha*, and *Kathetopodion*.

47. NUMBER OF ABDOMINAL SPIRACLES. (0) 8; (1) 2 or 3. Among most members of the Scaphidiinae, the number of abdominal spiracles has been reduced to three or two in

members of *Cyparium.* In some taxa (e.g., some members of *Scaphium* and *Cyparium*) the spiracles have atrophied, there are no associated air sacs, and they are probably not functional. The number of functional spiracles among species of scaphidiines requires detailed study and we have limited our observations to a small portion of dissected taxa. Reduction of the number of spiracles (1), with respect to the outgroup taxa, is inferred as apomorphic. This character is not observed in specimens *Euscaphidium*, *Cerambyciscapha*, and *Kathetopodion.*

48. Abdominal paratergites on segment 3 (Figs 7-9). (0) Present; (1) absent. Reduction of the number of paratergites is complicated and variable. We have probably oversimplified the coding of these character states, indicating only complete reduction of the paratergites: character state (1) indicates their complete absence, in contrast, character state (0) indicates presence of 1 or 2 paratergites. The distribution of the number of paratergites among members of the outgroup and ingroup is given in Table 2. We do not recognize serial homologies among paratergites because the comparisons made among segments reveal that character states between segments do not covary in a consistent way. Therefore we treat each segment separately in this and the following characters. We did not examine the structure of paratergites in specimens of *Cerambyciscapha* and *Euscaphidium.*

49. Abdominal paratergites on segment 4. (0) Present; (1) absent. See character 48 and Table 3.

50. Abdominal paratergites on segment 5. (0) Present; (1) absent. See character 48 and Table 3.

51. Abdominal paratergites on segment 6. (0) Present; (1) absent. See character 48 and Table 3.

52. Abdominal paratergites on segment 7. (0) Present; (1) absent. See character 48 and Table 3. This character is coded as polymorphic for the Apateticinae. Variation of this character and lack of phylogenetic information of the outgroup creates uncertainty in determining the polarity of this character.

53. Abdominal tergite 7 with oblique line. (0) Absent; (1) present. Among members of the Scaphiina, there is an oblique line present on the sixth tergite. This line is absent in some species of *Episcaphium*, and the character is coded as polymorphic for this taxon. Character state (1) is absent among members of the outgroup and it is, therefore, inferred as apomorphic.

54. Abdomen. (0) Parallel-sided; (1) narrowed posteriorly. The abdomen among members of the Scaphidiinae, Apateticinae, and Trigonurinae is narrowed posteriorly. Among members of the Piestinae and other oxyteline group taxa, the abdomen is parallel-sided. It is likely that character state (0) is primitive, however, the phylogenetic relationships are not known for the outgroup taxa, and character state (1) may be plesiomorphic. Therefore, polarity of this character is equivocal.

55. Length of abdominal sternite 3. (0) Equal to that of the remaining sternites; (1) larger than that of the remaining sternites. Among members of the Scaphidiinae, several morphological characters of the abdomen covary; length of abdominal sternites 3 and 7 relatively large, abdomen shortened, and elytra covering most of the abdominal tergites. We code only one of these characters because of the likelihood of character non-independence. Character state (1) is absent in members of the outgroup and it is therefore inferred as apomorphic.

56. Abdominal sternite 7. (0) Without oblique line; (1) with oblique line. Among members of the Scaphidiina, Ascaphium, and some species of *Episcaphium*, there is an oblique line present on the fifth sternite. This character is coded as polymorphic for *Episcaphium*. This feature should not be confused with the line produced by the overlap of tergite onto sternite. Character state (1) is absent among members of the outgroup and it is, therefore, inferred as apomorphic.

57. Procoxa (Figs 4-6, 15, 16). (0) Transverse; (1) conical. The procoxa of Scaphidiinae are conical and projecting and the trochantin has become fused to the internal wall of the prothorax. In contrast, the procoxa among members of the outgroup is transverse and the trochantin is clearly visible in ventral view. Character state (1) is absent in members of the outgroup and it is inferred as apomorphic.

58. Mesotrochantin. (0) Exposed in ventral view; (1) `absent. Among members of the outgroup, the mesotrochantin is clearly visible and articulates with the mesocoxa. Among members of the Scaphidiinae the trochantin appears absent or its location enigmatic. There appears to be no trace of the trochantin on the mesocoxa, where it may have become fused with it; although, it is likely that the trochantin has become fused to the coxa and fusion has become so complete that evidence of the trochantin is no longer visible.

Another possibility is that the mesotrochantin has become fused to the mesosternum. On the mesosternum there is a feature that has been referred to in the past as the "mesepimeron" (see Leschen & *al.* 1990), which is an elongate sclerite located adjacent and parallel to the meso-metasternal suture, and has been confused with the true mesepimeron (A.F. Newton, personal communication). This sclerite may be marked internally by a ridge in some of the larger species of Scaphidiines or not in some smaller species. In addition, the line that marks the sclerite externally may be completely absent in some members of the Scaphisomatini. The "mesepimeron" may be the trochantin that has become incorporated into the mesosternite.

Regardless of the phylogenetic history of the trochantin, character state (1) is absent in members of the outgroup and it is, therefore, inferred as apomorphic.

59. Tibial stria (Fig. 11). (0) Absent; (1) present. Members of the Scaphidiina, *Ascaphium*, and *Episcaphium* have striae that run along the entire length of all the tibiae. This feature also occurs in members of the Apateticinae. Because the presence of character state (1) is in part of the outgroup, the polarity of this character is uncertain.

60. Tibial spines (Figs 28, 29). (0) Present; (1) absent. Well-developed spines distributed along the shaft of the tibia are present in members of the outgroup and *Cyparium*. The remaining members of the Scaphidiinae do not have well-developed spines on the tibia, only the presence of setae. Character state (1) is absent in the outgroup and it is therefore inferred as apomorphic.

61. Abdominal sternite 8 with anteriorly projecting process. (0) Absent; (1) present. Among members of *Cyparium* and *Scaphium*, there is a process arising from the anterior edge of the eighth sternite, which may serve as an attachment point for musculature. This process is not found among members of the outgroup, therefore character state (1) is inferred as apomorphic. This character is not observed in specimens of *Kathetopodion*.

62. Abdominal sternite 9 of male with well-defined sclerotized rim that is continuous anteriorly (Fig. 39). (0) Absent; (1) present. The abdominal ninth sternite of male specimens of Scaphidiinae is a tongue-shaped sclerite that has a well-defined sclerotized rim and is continuous about the anterior apex: the anterior apex is evenly arcuate. The form of the sternite is variable among members of the outgroup, and differ in form from that present among members of the Scaphidiinae. Members of the Apateticinae have the anterior apex separated into two lobes, and are not connected anteriorly. Among members of the Piestinae, the anterior apex is lyreform, and connected at the apex by a membrane. In specimens of *Trigonurus*, the apex is produced into two broad processes that are well-sclerotized. The primitive condition of the ninth sternite of males in the oxyteline group is unknown, however we consider that the form exhibited among members of the Scaphidiinae is substantially different from that occurring among the outgroups, and, therefore, character state (1) is inferred as apomorphic. Male specimens of *Kathetopodion* are unknown.

63. Abdominal sternite 10 of male narrowed anteriorly forming a style-like process. (0) Absent; (1) present. The tenth sternite of male specimens of Scaphidiinae is relatively narrow with the anterior portion produced into an elongate style-like process. Among members of the outgroup the anterior portion of the tenth sternite is not produced into a narrow process and is broadly arcuate or slightly constricted. Character state (1) is absent among members of the outgroup and it is, therefore, inferred as apomorphic. Male specimens of *Kathetopodion* are unknown.

64. Orientation of the apex of aedeagus. (0) Posteriorly; (1) ventrally. The apex of the median lobe of the aedeagus among members of the Scaphidiina is bent down towards the ventral portion of the aedeagus (in some taxa the aedeagus has rotated 90° from its original position in the abdomen). Among members of the outgroup and the remaining scaphidiine taxa, the median lobe of the aedeagus is directed posteriorly. Character state (1) is absent among members of the outgroup and it is considered apomorphic. Male specimens of *Kathetopodion* are unknown.

65. INTERNAL SAC BENEATH THE PENIS VALVES. (0) Exposed; (1) hidden. Among members of the Scaphidiina the internal sac is concealed beneath the lobes of the penis valves and can only be seen in cleared specimens. Among members of the outgroup the ejaculatory duct is exposed suggesting that character state (1) is apomorphic. Male specimens of *Kathetopodion* are unknown.

66. SCLERITES OF INTERNAL SAC OF AEDEAGUS. (0) Asymmetrical; (1) symmetrical. Among members of the Scaphidiina, exclusive of *Cerambyciscapha*, the internal sac of the aedeagus contains bilaterally symmetrical sclerites. Among members of the remaining Scaphidiinae and the outgroups, the internal sacs of males have asymmetrical sclerites. Character state (1) is absent in the outgroup and it is, therefore, inferred as apomorphic. Male specimens of *Kathetopodion* are unknown.

67. COMPRESSOR PLATE OF AEDEAGUS DISTINCT BEYOND LEVEL OF THE ARTICULATIONS OF THE PARAMERES. (0) Not distinct beyond level of the articulations of the parameres; (1) distinct beyond the level of the articulations of the parameres. Among members of the Scaphidiina the compressor plate of the aedeagus is large and distinct. Among members of the outgroup taxa the compressor plate does not extend beyond the level of the articulations of the parameres and, therefore, character state (1) is inferred as apomorphic. Male specimens of *Kathetopodion* are unknown and this character is coded as unknown in *Cerymbyciscapha*.

68. GONOCOXITE IN CROSS-SECTIONAL VIEW. (0) Flattened; (1) rounded. The form of the gonocoxite among members of the outgroup is flattened in cross-section. In contrast, the form of the gonocoxites among members of the Scaphidiinae is rounded in cross-section. Character state (1) is absent in the outgroup and is, therefore, inferred as apomorphic. This character is not observed in the specimens of *Kathetopodion*, *Euscaphidium* and *Cerambyciscapha*.

69. GONOSTYLE (Figs 35-38). (0) Short; (1) long. Among members of the Scaphisomatini and the outgroup, the gonostyle is less than 3 times as long as wide (Figs 36, 37). Among members of *Cyparium*, *Ascaphium*, and *Episcaphium*, the gonocoxite is 3 times as long as wide. Character state (1) is absent among the outgroup taxa and it is inferred as apomorphic. This character is not observed in the specimens of *Kathetopodion*, *Euscaphidium* and *Cerambyciscapha*.

Table 1

Old and newly proposed classifications of the Scaphidiinae based on Newton and Thayer (1992) and this study.

Current Classification	Proposed Classification
Cypariini Achard, 1924	Cypariini Achard, 1924
Heteroscaphini Achard, 1914	Scaphiini Achard, 1924
Scaphidiini Latrielle, 1807	Scaphidiini Latrielle, 1807
Cerambyciscaphina Pic, 1915	Scaphisomatini Casey, 1894
Diateliina Achard, 1924	Heteroscaphina Achard, 1914
Scaphidiina Latreille, 1807	Baeoceridiina Achard, 1924
Scaphiina Achard, 1924	Baeocerina Achard, 1924
Scaphisomatini Casey, 1894	Scaphisomatina Casey, 1894
Baeoceridiina Achard, 1924	Toxidiina Achard, 1924
Baeocerina Achard, 1924	
Scaphisomatina Casey, 1924	
Toxidiini Achard, 1924	

Table 2

Number of sclerotized paratergites present in the abdomen among members of the Scaphidiinae and taxa used as outgroups. Specimens of *Euscaphidium* and *Cerambyciscapha* were not examined.

Abdominal segment	3	4	5	6	7
			Number of paratergites		
Scaphidiinae					
Ascaphium	0	2	2	2	0
Episcaphium	0,1	2	2	2	0
Scaphium	2	2	2	2	0
Scaphidium	0	0	0,1	1	0
Diatelium	0	1	1	1	0
Cyparium	2	2	2	2	0
Kathetopodion	0	0	0	0	0
Scaphisomatini	0	0,1	0,1	0	0
Outgroup taxa					
Apatetica	2	2	2	1	0
Nodynus	2	2	2	2	1
Siagonium	2	2	2	2	1
Zirophorus	1	1	1	1	1
Trigonurus	1	1	1	1	1

TABLE 3

Data matrix used for the cladistic analysis of Scaphidiinae. Character numbers correspond to those mentioned in the text. An * indicates a character state coded as a polymorphism.

	Characters						
	1	2	3	4	5	6	
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	123456789
Ascaphium	1111101110	0110111111	1101110010	1101110111	0111011100	0111111111	011000011
Episcaphium	1111101110	011°111**1	11011110*0	*1011*0111	0111011100	01*11*1111	011000011
Scaphium	1111101110	0100111100	1101111010	1101110111	011*011000	0111101101	111000010
Euscaphidium	1111111120	01111?1111	1101110021	01?10011??	1111??????	??01111111	0111111??
Scaphidium	1111111120	011110111*	110111*021	0111*01110	1111111111	0101111111	011111100
Cerambyciscapha	1111111010	01111??111	1101110021	01110011??	0111??????	??01111111	011110???
Diatelium	1111111120	01121?1011	1101110021	0111001110	0111111100	0101111111	011111100
Cyparium	1111101100	0101101000	1111110020	1101110111	0101011000	0101101100	111000001
Kathetopodion	1100011121	11011?0100	1111210110	01?000?1??	?101???111	1101101101	?????????
Scaphisomatini	111*1*11**	*1*11****0	11112101*0	**0***0*1*	01**111111	11°1101101	011000010
Piestinae	0001000100	0000*00000	1000000000	000100000*	0011000000	0000000000	000000000
Apateticinae	0000000000	0000000000	*000000000	100*000000	0000000000	0*01000010	000000000
Trigonurinae	0000000000	0000000000	0001000000	0000000000	0000000000	0001000000	000000000

RESULTS AND DISCUSSION

Cladistic analysis that used a generalized outgroup (GENGROUP) resulted in one most parsimonious cladogram (Fig. 40) with the following characteristics: TL = 90, CI = 0.744, and RI = 0.736. Cladistic analysis of the Scaphidiinae that used all three outgroups (ALLGROUP) simultaneously to polarize characters in the PAUP runs resulted in one cladogram (Fig. 41B) with the following characteristics: Tree length (TL) = 104, Consistency index (CI) = 0.702, Retention index (RI) = 0.806. Fig. 40 shows the most parsimonious cladogram resulting from GENGROUP analysis with the distribution of all the characters used in the analysis.

Among those characters with uncertain polarity assignments in the character analysis those for which the polarity is opposite of that originally proposed are characters 4, 8 (an autapomorphy for *Cerambyciscapha*), and 34 (when ALLGROUP and GENGROUP are used), and characters 31 and 40 (when GENGROUP is used). The polarity of character 43 remains equivocal in all analyses. Characters 21, 44, and 54 are uninformative regardless of outgroup specification and characters 15, 24, 52, and 54 are uninformative in the analysis that used GENGROUP (exclusive of those characters that occur as synapomorphies of Scaphidiinae).

Regarding the choice and formulation of outgroup taxa, it is, of course, the best option to have a well-defined sister taxon and outgroup structure for polarizing the characters of the ingroup (MADDISON & *al.*, 1984; NIXON & CARPENTER, 1993). However, some putative synapomorphies can be uninformative when specifying a generalized outgroup. For example, some potentially important synapomorphies (characters 15, 24, and 54) for the Scaphidiinae were uninformative when GENGROUP was used because these characters are distributed in the basal portion of the cladograms and are codified as uncertain in the outgroup. On the other hand, putative synapomorphies distributed higher in the cladogram (e.g., characters 34, 43, and 59) are not affected by ambiguous polarity in the analysis using GENGROUP.

The number of paratergites among the Scaphidiinae is very variable, suggesting that this set of characters is weak in their phylogenetic information. Also, we may have oversimplified the coding and homologies of the paratergal character states. Therefore, we investigated the performance of these characters in the cladistic analyses. If characters 48 - 52 (see character analysis) are removed from the data matrices, and the analyses repeated, the same topologies as that in Figs 40 and 41 are produced regardless of type of outgroup. On the basis of these analyses the paratergal characters do not affect the relationships among the tribes and subtribes.

Among the two topologies of the cladograms produced by the above analyses, there is strong evidence that most family group taxa are monophyletic. However, the Scaphidiini (including the Cerambyciscaphina, Diateliina, Scaphiina, and Scaphidiina) are paraphyletic with respect to the placement of the Cypariini and Scaphisomatini (including *Kathetopodion*), and with respect to each other (Fig. 41). The phylogenetic placement of the Cypariini is somewhat enigmatic. It is either placed at the base of the Scaphidiinae, as sister taxon of the remaining members of the subfamily, or forms a clade with members of Scaphidiina.

On the basis of the consistent patterns revealed by the phylogenetic analyses discussed above we make the following changes in the higher classification of the Scaphidiinae. We elevate the subtribes Scaphiina and Scaphidiina to tribal status, and the monotypic subtribes Cerambyciscaphina and Diateliina included in the Scaphidiina are eliminated, such that *Cerambyciscapha* and *Diatelium* are placed into the Scaphidiini.

Leschen (1993) proposed relationships for North American genera of Scaphidiinae based upon larval and adult characters. Three trees that were produced from his study exhibit similar conflicts among relationships for representatives of the Cypariini, Scaphidiini, and Scaphiini, although the Scaphisomatini were always placed as a derived taxon. Adequate tests for the relationships proposed in this study can be made by additional information gathered from other characters that may be useful for phylogenetic reconstruction. Therefore it is necessary to procure more larval and adult material, and information from live specimens (fungal hosts, habitats, mating behaviours, etc.) and add this information to our data set to test the phylogenetic hypotheses we propose.

Tribe Scaphiini

The Tribe Scaphiini is monophyletic based on the presence of two unambiguous synapomorphies: endocarina at base of head present along half of the length of the gular region (16) and abdominal tergite 7 with an oblique line (53). Two characters supporting this clade are: head with a neck (14) and presence of a transverse mesosternal ridge (27).

The sister relationship between *Ascaphium* and *Episcaphium* is well supported by several characters (Fig. 40).

TRIBE SCAPHIDIINI

The tribe Scaphidiini is well supported in our analysis by the following unambiguous synapomorphies: eye notched (13), posterior angle of the prothorax molded onto the anterior angle of the elytron (19), presence of a basal stria on the pronotum (20), mesothorax with an anterior process (30), metasternum with a median longitudinal line (33) and male setiferous sex patch (37), abdominal sternite with an oblique line (56), presence of tibial striae (59), apex of aedeagus oriented ventrally (64), and internal sac hidden beneath penis valves (65). Concordant with these characters are the width of mesosternal process more than that of mesocoxa (29-2), compressor plate of aedeagus distinct beyond level of articulation of the parameres (67), and gonocoxite flattened in cross-sectional view (68-0).

The relationships among the genera of Scaphidiini are supported by relatively few characters, although the sister relationship between *Euscaphidium* and *Scaphidium* is supported by one unique unreversed character (presence of prescutal stridulatory files in males (41)). Likewise, *Diatelium* is sister taxon of these based on a unique and unreversed character (internal sclerites of the aedeagus symmetrical (66). Because so few specimens of *Euscaphidium* and *Cerambyciscapha* are available for study and these are known only from one sex, many characters were scored as unknown in the data matrix. The discovery of additional specimens of these will provide useful data that will fill gaps in our knowledge of certain character states and ultimately test the relationships we proposed in this study.

TRIBE SCAPHISOMATINI

The tribe Scaphisomatini is the largest family group taxon among Scaphidiinae and the relationships among its members are largely unknown. There is adequate data that suggest that *Kathetopodion* is a member of this tribe based on four unambiguous synapomorphies: prosternum in front of coxa reduced to length shorter than that of procoxa (23), procoxal cavities internally closed by the fusion of the prosternum and hypomeron (25-2), mesosternum with an anvil-like process (28), and abdominal paratergites absent from segment 6 (51). Concordant with these characters are: mandible with one tooth on the incisor lobe (4-0), antennomeres 3-11 asymmetrical (10), shape of mentum wider than long (17-0), premetacoxal lines present on metasternum (34-0), and epipleuron in lateral view oblique (43-0). These characters are variable among members of Scaphisomatini and whether these are truly synapomorphies will only be determined by a detailed cladistic analysis of the tribe at the generic level.

TRIBE CYPARIINI

The monogeneric tribe Cypariini is supported by the following unambiguous synapomorphies: prosternum in front of procoxae reduced to a length less than that of procoxa (23), abdominal sternite 8 with anteriorly projecting process (61), and gonostyle long (69). Concordant with these is the width of the mesosternal process more than that of mesocoxa (29-2).

KEY TO THE GENERA OF THE SCAPHIDIINAE, EXCLUDING THE SCAPHISOMATINI

1. Antennal segments 3 to 11 filiform and/or flattened and asymmetrical, usually smaller species. . . . . Scaphisomatini
- Antennal segments not filiform, symmetrical, usually larger species. 2
2. Antenna with antennomeres of club round and compact (Fig. 14). 3
- Antenna with anntenomeres of club flattened and loose. . . . . (Scaphidiini) 6
3. Anterior portion of prosternum reduced (Figs 15, 31), smaller than 1/3 width of coxa, pro- and mesotibia with conspicuous raised spines (Figs 28, 29). . . . . (Cypariini) *Cyparium*
- Anterior region of prosternum prolonged (Fig. 16), longer than 1/3 coxal width, pro- and mesotibia without conspicuous spines. . . . . (Scaphiini) 4
4. Eyes entire not emarginate, metatarsus with tarsomere 1 about as long as 2. . . . . *Scaphium*
- Eyes emarginate, metatarsus with tarsomere 1 much longer than 2. 5
5. Mesosternal ridge present (Fig. 12). . . . . *Episcaphium*
- Mesosternal ridge absent. . . . . *Ascaphium*
6. Antenna elongate, longer than length of body. . . . . *Cerambyciscapha*
- Antenna shorter than length of body. 7
7. Neck present and elongate (Fig. 1). . . . . *Diatelium*
- Neck absent. 8
8. Posterior angle of prothorax strongly extended and pointed, lateral margin of prothorax strongly sinuate, anterior region of elytra rugose (Fig. 1a) . . . . *Euscaphidium*
- Posterior angle of prothorax not strongly extended and pointed, lateral margin of prothorax not sinuate, elytra not rugose. . . . . *Scaphidium*

CYPARINI Achard, 1924

Cypariini Achard, 1924
Type genus: *Cyparium* Erichson, 1845

Cyparium Erichson, 1845 (Figs 13-15,28,29,31,35)

Type species: *Cyparium palliatum* Erichson, 1845, by monotypy.
Yparicum Achard, 1920. Type species: *Yparicum yunnanum* Achard,1920, by monotypy. Synonymy by Löbl (1992).

DESCRIPTION. - Length 2.5-6.5 mm. Hypopharynx with scattered pores, microtrichia composed of equal sizes. Terminal labial palpus not inserted subapicaly into penultimate palpus. Galea without subapical short bristles, galeal process not well-developed. Labral setae thickened. Antenna (Fig. 14) not filiform, antennomeres of club rounded and compact. Scrobal setae 4. Eye not emarginate. Head not prolonged beyond eyes, without distinct tempora. Gular carina distinct along length of suture. Proventriculus with 6 rods, setae not observed. Pronotum with posterior angle pointed, loosely pressed to sides of elytra, sub-basal stria absent. Anterior portion of prosternum greatly reduced. Mesosternal ridge (Fig. 13) present. Mesocoxal cavities separated by more than coxal width. Process on prepectus absent. Submesocoxal lines (Fig. 13) connected. Longitudinal line on metasternum present. Metacoxae transverse. Intermetacoxal plate present. Metasternal setae present. Male metasternum without setose patch. Metasternum without paired impressions, costae or tubercles. Metendosternite constricted beyond point of anterior tendon attachment, basal piece carinate dorsally. Male without prescutal files. Epipleuron slightly horizontal. Posterior margin of elytra serrate. Elytral interlocking mechanism of the tongue-in-groove type. Wing vein 3 absent, vannal lobe absent. Spiracles 4-8 absent or nonfunctional, abdominal spiracle 3 not in membrane. Oblique line of abdominal sternite 7 absent. Femora and tibia with spines.

Male. - Metasternite with paired intermetacoxal processes in some species. Abdominal sternite 9 with anterior process. Aedeagus resting on its side, apex bent downwards, orifice exposed, valves overlapping, with three well-developed lobes of the median lobe, internal sac without complex symmetrical sclerites, compressor plate not distinct.

Female. - Coxite (Fig. 35) flattened in cross section, with lateral long setae. Style elongate without 2 long apical setae.

Comments. - The 48 species of *Cyparium* are relatively homogenous in external and aedeagal characters. Most species are uniform in colour (black or light brown), however, some tropical species are spotted or have apical bands on the elytra. A key to the Asian species is provided by Löbl (1991). Males of some species have paired processes originating from the posterior margin of the metasternal process.

Distribution. - Almost world wide; Absent from oceanic islands, northern Africa, Australia, Europe, Madagascar, New Guinea and Chile.

Larval descriptions. - *Cyparium sibiricum*, (Kompantsev & Pototskaya, 1987), general description, (Newton, 1991).

Biology. - Specimens of adults and larvae have been collected mainly from Agaricales (Newton, 1984; Kompantsev & Pototskaya, 1987), but have also been reared from coral fungi (Clavaraceae) and tooth fungi (Hydnaceae). Records from coral fungi include the North American species *Cyparium terminale* (from ?*Clavaria*; Newton, 1984) and an undetermined Peruvian species (from *Pterula* sp.; Leschen, personal observation). In both instances larvae were present and/or reared. Once *C. terminale* was reared from the fungus *Tremellodendron pallidum*, a persistent coral-like fungus in the Tremellales (Leschen, 1988). Larvae feed mainly on the hyphae of these fungi (Newton, 1984).

Scaphiini Achard, 1924

Scaphiitae Achard, 1924
Type genus: *Scaphium* Kirby, 1837

Description. - Hypopharynx with central pores, setae of equal sizes (Fig. 21). Terminal labial palpus inserted subapically into penultimate palpus. Galea without subapical setae, galeal process not well developed. Labral setae not thickened. Antenna not filiform, club loose, slightly or not flattened. Scrobal setae 4. Head prolonged beyond eyes with distinct tempora, gular carina distinct basally. Proventriculus with 8 rods and setose. Anterior portion of the prosternum elongate. Pronotal angle usually rounded. Prepectus without process. Male without prescutal files or setal patch. Scutellum 1/3 width of entire mesonotum. Metasternum with single seta, median longitudinal line and male setose patch absent, paired impressions or costae or tubercles present or not. Intermetacoxal plate present (Fig. 16). Metacoxae not strongly transverse. Metendosternite (Fig. 34) carinate basally, dorsal arms not constricted above insertion of anterior tendon. Epipleuron vertical. Elytral interlocking mechanism of the tongue-in-groove type. Abdominal spiracle 3 in membrane. Femora and tibia without spines.

Male. - Aedeagus resting on its side, apex bent downward, orifice not exposed, valves usually overlapping, basal bulb without three sclerotized lobes, internal sacs without complex asymmetrical sclerites, compressor plate not distinct beyond level of paramere articulation.

Female. - Coxite (Fig. 38) cylindrical in cross section, lateral long setae absent. Style elongate, without two long setae.

Ascaphium Lewis, 1893

Type species: *Ascaphium sulcipenne* Lewis, 1893, designated by Löbl (1992).

Description. - Length 3.5-7.0 mm. Eye emarginate. Antennal club loose, not flattened. Posterior pronotal angle rounded, loosely molded to elytra. Sub-basal stria of pronotum present. Mesosternal ridge absent. Mesocoxal cavities not separated more than coxal width. Submesocoxal lines connected. Elytron with deep stria, posterior edge serrate. Anal vein 3 absent. Spiracles 4-8 absent and/or nonfunctional. Oblique line on sternite 7 absent. Intermetacoxal process of male absent. Male sternite 8 without anterior process. Female coxite without long lateral setae. Metatibia of male not curved. Metatarsomere 1 longer than 2.

Comments. - The 7 known species of *Ascaphium* are uniformly black. The pattern of the elytral stria are important characters for species identification and they can be identified with the key given by Löbl (1992).

Distribution. - Eastern Palaearctic and southeast Asia.

Biology. - The Japanese species *Ascaphium sulcipenne* and *A. tibiale* have been collected from *Trametes versicolor* and other polypore fungi (T. Nakane, personal communication).

Episcaphium Lewis, 1893 (Fig. 38)

Type species: *Episcaphium semirufum* Lewis, 1893, by monotypy.

Phenoscaphium Achard, 1922b. Type species: *Phenoscaphium callosipenne* Achard, 1922b, by monotypy. **Syn. nov.**

Description. - Length 4.5-7.0 mm. Eye emarginate. Antennal club loose, flattened. Posterior pronotal angle rounded or not, and tightly molded to elytra. Subbasal stria of pronotum present. Mesosternal ridge present. Mesocoxal cavities separated by more than coxal width. Submesocoxal lines connected or not. Posterior edge of elytra serrate or not. Wing with vannal lobe and vein 3 absent. Spiracles 5-8 absent and/or nonfunctional. Oblique line of abdominal sternite 7 present or absent. Intermetacoxal process of male absent. Male sternite 8 without anterior process. Female coxite with long lateral setae. Metatibia of males not curved. Metatarsomere 1 longer than 2.

Comments. - Achard (1922b) described the species *Phenoscaphium callosipenne*, placing it in a genus separate from *Episcaphium*. He erected this genus based on the antennal club which is not flattened with the segments widened abruptly from the base and the posterior angle of the pronotum pointed and weakly extended behind. Achard also recognized that the elytra are relatively shorter in this species and that the elytral surface is uneven and irregular. We believe that Achard was incorrect in recognizing *Phenoscaphium* as a separate genus because the characters he used are either variable (antennal characters and posterior pronotal angle) or autapomorphies (elytral surface irregular). Therefore we place *P. callosipenne* in the genus *Episcaphium.*

Species of *Episcaphium* can be identified with the key provided by LÖBL (1992). The species *E. callosipenne* is not included in this key but can be distinguished by the remaining species by its black colouration, the submesocoxal lines connected at the middle, and by the uneven surface of the elytral disc.

Distribution. - Eastern Palaearctic and southeast Asia.

Biology. - Specimens of *E. semirufum* have been collected from fungus covered rotten logs and from polypores (I. Löbl, personal observation, S.I. Naomi and T. Nakane, personal communications).

Scaphium Kirby, 1837 (Figs 16,21,23,24,26,34)

Type species: *Scaphium castanipes* Kirby, 1837, by monotypy.

Description. - Length 4.5-7.0 mm. Eyes entire. Antennal club loose, antennomeres not flattened. Posterior pronotal angle rounded, not molded tightly onto elytra. Sub-basal stria of pronotum absent. Mesosternal ridge present. Mesocoxal cavities not separated more than coxal width. Submesocoxal lines connected. Posterior edge of elytra with or without serrations. Anal vein 3 present. Spiracles 5-8 absent and/or nonfunctional. Oblique line on abdominal sternite 7 absent. Intermetacoxal process of male present. Male sternite 8 with anterior process. Female coxites with lateral long setae. Metatibia curved in males. Metatarsomere 1 as long as 2.

Comments. - The four species included in *Scaphium* are entirely black in colour. *Scaphium immaculatum* can be distinguished from the other species by its well developed metasternal process in the male which is produced posteriorly into two large flattened processes. Examination of the single type from Paris revealed that the generic placement of *Scaphium ferrugineum* is certain but that the distribution record from South African is dubious. Males of *Scaphium* have curved tibia and intermetacoxal processes, and in some species there may be paired impressions on the metasternum.

Distribution. - Holarctic, ?South Africa.

Larval descriptions. - *Scaphium quadraticolle*, (KOMANTSEV & POTOTSKAYA 1987); *Scaphium castanipes*, (ASHE, 1984), general description, (NEWTON, 1991).

Biology. - Species of *Scaphium* have been associated with members of Agaricales (ASHE, 1984; KOMANTSEV & POTOTSKAYA, 1987). NEWTON (in ASHE, 1984) noted that larval specimens that may be members of *Scaphium* from Alaska, had guts filled with fine fungus mycelium.

SCAPHIDIINI Latreille, 1807

Scaphidiina Latreille, 1807
Scaphiitae Achard, 1924
Type genus: *Scaphidium* Olivier, 1790
Cerambyciscaphini Pic, 1915b. Type genus: *Cerambyciscapha* Pic, 1915b. **Syn. nov.**
Cerambyscaphini Achard, 1924 (misspelled type genus *Cerambyscapha* Pic, 1915b).
Diateliina Achard, 1924. Type genus: *Diatelium* Pascoe, 1863. **Syn. nov.**

Description. - Hypopharynx (Figs 20, 30) with sensory pores scattered on surface, setae of different sizes. Terminal labial palpus with terminal segment subapically inserted into the penultimate palpus. Galea (Fig. 27) with subapical setae. Labral setae thickened (Fig. 25). Eye emarginate. Antennal club loose and flattened. Head not extended beyond eyes, without distinct tempora. Gular carinae internally distinct throughout. Proventriculus with 8 rods and not setose. Posterior pronotal angles tightly molded to elytra. Anterior portion of prosternum reduced. Mesocoxal cavities separated by a distance more than the coxal width. Prepectus with an anterior process. Submesocoxal lines not connected. Metasternum with a median longitudinal line (not observed in *Euscaphidium*), discal setae absent, never with paired impressions, costae or tubercles. Intermetacoxal plate absent. Metacoxa not very transverse. Metendosternite with dorsal arm constricted beyond point of attachment of anterior tendons, basal piece not carinate dorsally (not observed in *Euscaphidium* and *Cerambyciscapha*). Scutellum about 1/2 width of entire mesonotum. Epipleuron vertical. Posterior edge of elytra serrate. Elytral interlocking mechanism evenly undulate (not observed in *Euscaphidium* and *Cerambyciscapha*). Abdominal spiracle 3 in membrane. Spiracles 4-8 absent and/or nonfunctional (not observed in *Euscaphidium* and *Cerambyciscapha*). Oblique line on abdominal sternite 5 present. Femora and tibia without spines.

Male. - Metasternum with setose patch. Abdominal sternite 8 without anterior process. Aedeagus with apex not bent downward, orifice exposed, valves not overlapping, basal bulb without three sclerotized lobes, compressor plate distinct beyond paramere articulation (latter unclear in *Cerambyciscapha*).

Female - (no data for *Euscaphidium* and *Cerambyciscapha*). Coxite flattened in cross section, not cylindrical, with lateral long setae. Style short with 2 long setae.

Euscaphidium Achard, 1922a (Fig. 1a)

Type species: *Euscaphidium tuberosum* Achard, 1922a, by monotypy.

Description. - Length 8.0 mm (Sumatran specimen). Galeal process well developed. Antenna not filiform, antennal club flattened, insertion not raised. Scrobal setae 6. Neck not prolonged behind. Pronotum with sub-basal stria present. Lateral pronotal margin sinuate, posterior angle pointed. Prosternum horizontal. Mesosternal keel present, ridge absent. Male with prescutal files. Elytra with lateral humeral lobe. Condition of wing not observed. Mesotibia with curved apical spines. Internal sac of aedeagus with complex symmetrical sclerites. Orientation of aedeagus not observed in this species.

Comments. - Known from two male adult specimens.

Distribution. - Sumatra and Borneo.

Scaphidium Olivier, 1790 (Figs 3,5,8,10-12,17-19,27,30,32)

Type species: *Scaphidium quadrimaculatum* Olivier, 1790, designated by Leach, 1815.
Ascaphidium Pic, 1915a. Type species: *Ascaphidium sikorai* Pic, 1915a, by monotypy. **Syn. nov.**
Cribroscaphium Pic, 1920 (sg.). Type species: *Scaphidium irregulare* Pic, 1920, by monotypy. **Syn. nov.**
Hemiscaphium Achard, 1922a. Type species: *Scaphidium striatipenne* Gestro, 1880, by original designation. **Syn. nov.**
Hyposcaphidium Achard, 1922a (sg.). Type species: not designated.
Isoscaphidium Achard, 1922a (sg.). Type species: not designated.
Pachyscaphidium Achard, 1922a (sg.). Type species: *Scaphidium arrowi* Achard, 1920, by original designation.
Scaphidiolum Achard, 1922a. Type species: *Scaphidium basale* Castelnau, 1840, by original designation. **Syn. nov.**
Scaphidopsis Achard, 1922a. Type species: *Scaphidium pardale* Castelnau, 1840, by original designation. **Syn. nov.**
Falsoascaphidium Pic, 1923. Type species: *Scaphidium subdepressum* Pic, 1921, by original designation. **Syn. nov.**
Parascaphium Achard, 1923: Type species: *Scaphidium optabile* Lewis, 1893, by monotypy. Synonymy by Löbl (1968).

Description. - Length 3.0-11.0 mm. Galeal process present, well-developed. Antenna filiform or not, club flattened, insertion not raised. Scrobal setae 4. Neck not prolonged behind. Posterior pronotal angle pointed, lateral margin not sinuate. Prosternum horizontal. Pronotum with sub-basal stria present or absent. Mesosternal ridge (Fig. 12) present or absent, keel present. Male with prescutal files (Figs 17, 32). Elytron without lateral humeral lobe. Anal vein 3 absent. Mesotarsi with straight apical spines. Aedeagus resting on its side or horizontal. Internal sac with complex symmetrical sclerites.

Comments. - The genera placed by us in synonymy with *Scaphidium* have been previously based upon characters that vary considerably and without well-defined syn- or autapomorphies.

Ascaphidium was erected by Pic (1915a) for species occurring in Madagascar and is based on relative lengths of antennal segments 5 and 6, punctation of the pronotum and elytra, and the convex form of the elytra. These characters vary within members of *Scaphidium*. Although members of *Ascaphidium* are easily recognized by their strikingly punctate dorsal surfaces, the degree of punctation varies among its included species and strong punctation is present in other species of *Scaphidium* that do not occur in Madagascar.

Cribroscaphium - Pic (1920), *Falsoascaphidium* Pic (1923), and *Scaphidiolum* Achard (1922a), were described based upon the relative degree of curvature of the pronotum, striae on the body, form of the antennal club, size of the scutellum, and other characters that either vary considerably among members of *Scaphidium* or are consistent for all members of the genus. Members of these groups do not have characters that readily separate them from other members of *Scaphidium*, although many species of *Scaphidiolum* have strongly narrowed frons.

Scaphidopsis Achard (1922a) was erected for species of *Scaphidium* occurring in South America that mainly have a well-developed pronotal hump and a mesosternal keel. These features are present in many members of *Scaphidium*, and although the relative size of the pronotal hump varies among members of the genus, it is relatively large in the type species *S. pardale* compared to most New World members of the genus.

Members of *Hemiscaphium* were recognized by ACHARD (1922a) mainly by the width of the head, which is larger than that of the anterior portion of the prothorax, and by the relative length of the antenna. This latter feature is variable among members of *Scaphidium*. Members of *Hemiscaphium* are distinct, however, and the relative width of the head is associated with the size of the eyes and anterior width of the pronotum, which is variable among members of *Scaphidium*.

New combinations resulting from the above synonymies are given in the Appendix. *Scaphidium* exhibits notable variation, especially the size of the body and eyes, colouration, pronotal features, elytra punctation, mesosternal characters, and male secondary sexual characters. Division of the 269 species of *Scaphidium* into natural species-groups will require a thorough analysis of all of the inclusive species and is outside the goals of this paper.

Distribution. - World wide, except for oceanic islands, New Zealand and southern South America.

Larval descriptions. - *Scaphidium amurense* (KOMPANTSEV & POTOTSKAYA, 1987); *S. quadrimaculatum* (KASULE, 1968; KOMPANTSEV & POTOTSKAYA, 1987); general description (NEWTON, 1991).

Biology. - Adult and larval fungal host records were reviewed by NEWTON (1984). Most species of *Scaphidium* are associated with lignicolous fungi, grazing mainly on encrusting hymenomycetes. Observations on Neotropical taxa support these data (Leschen, personal observation).

Adults of *Scaphidium* exhibit a wide degree of variation (large eyes, sexual dimorphism, etc.) which suggests a wide array of adult behaviors. Larval behaviors may also be variable. NEWTON (1984) reported that larvae from an undetermined species in Panama observed on a white resupinate polypore lived in tunnels among the fungus or wood and emerged at night to feed. LESCHEN (1993a) notes that larvae of another undetermined species from Mexico constructed retreats of frass from which individuals would emerge to feed during the day on the hymenium of an undetermined orange polypore.

Cerambyciscapha Pic, 1915b (Figs 20, 25, 39)

Type species: *Cerambyciscapha dohertyi* Pic, 1915b, by monotypy.

Description. - Length 6.5 mm (known specimen). Galeal process poorly-developed. Antenna filiform without antennal club, insertion raised. Scrobal setae 4. Head not prolonged behind. Posterior pronotal angle pointed. Pronotum with sub-basal stria present, lateral margins not sinuate. Prosternum horizontal. Mesosternal keel absent. Male without prescutal files. Mesosternal ridge absent. Condition of wing not observed in this species. Elytra without lateral humeral lobe. Mesotarsi with straight apical spines. Aedeagus on side. Internal sac without complex symmetrical sclerites.

Comments. - Known from a single male specimen.

Distribution. - Borneo.

Diatelium Pascoe, 1863 (Fig. 1)

Type species: *Diatelium wallacei* Pascoe 1863, by monotypy.

Description. Length 13-20 mm. Galeal process poorly developed. Antennae not filiform, antenal club loose and flattened, insertion not raised. Scrobal setae 10. Head (Fig. 1) prolonged behind eyes. Pronotal angle rounded. Pronotum with sub-basal stria present, lateral margin not sinuate, male with distinct anteriodorsal notch. Prosternum vertical. Mesosternal ridge absent, keel present. Male without prescutal files. Elytra without lateral humeral lobe. Anal vein 3 present. Mesotarsi with straight apical spines. Aedeagus on side. Internal sac with complex symmetrical sclerites.

Comments. - Status of the variety *D. wallacei*, var. *laterale* Achard (1920) is unknown.

Both sexes of *D. wallacei* have elongate necks, but the length of the male neck is usually longer, up to two times the length of the body. Males also differ in the form of the prothorax; the anterior portion of the pronotum is furnished with a notch, the pronotal volume is larger (Fig. 1), and the prosternum is narrow and is vertical in position. A dissection of a male revealed two large tendons that extend from the base of the neck to the sternum near the procoxae.

Distribution. - Borneo, Sulawesi, and Sumatra.

Biology. - Achard (1920) briefly mentioned that *D. wallacei* was collected from fungi growing on a trunk of a tree.

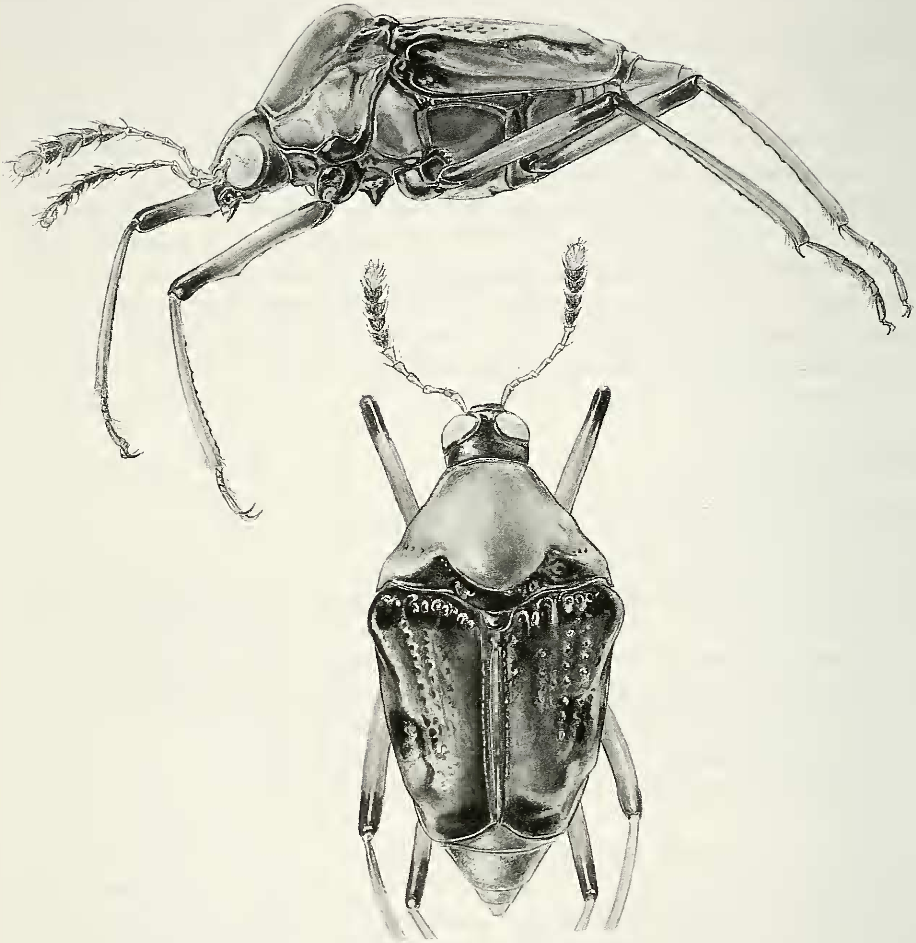
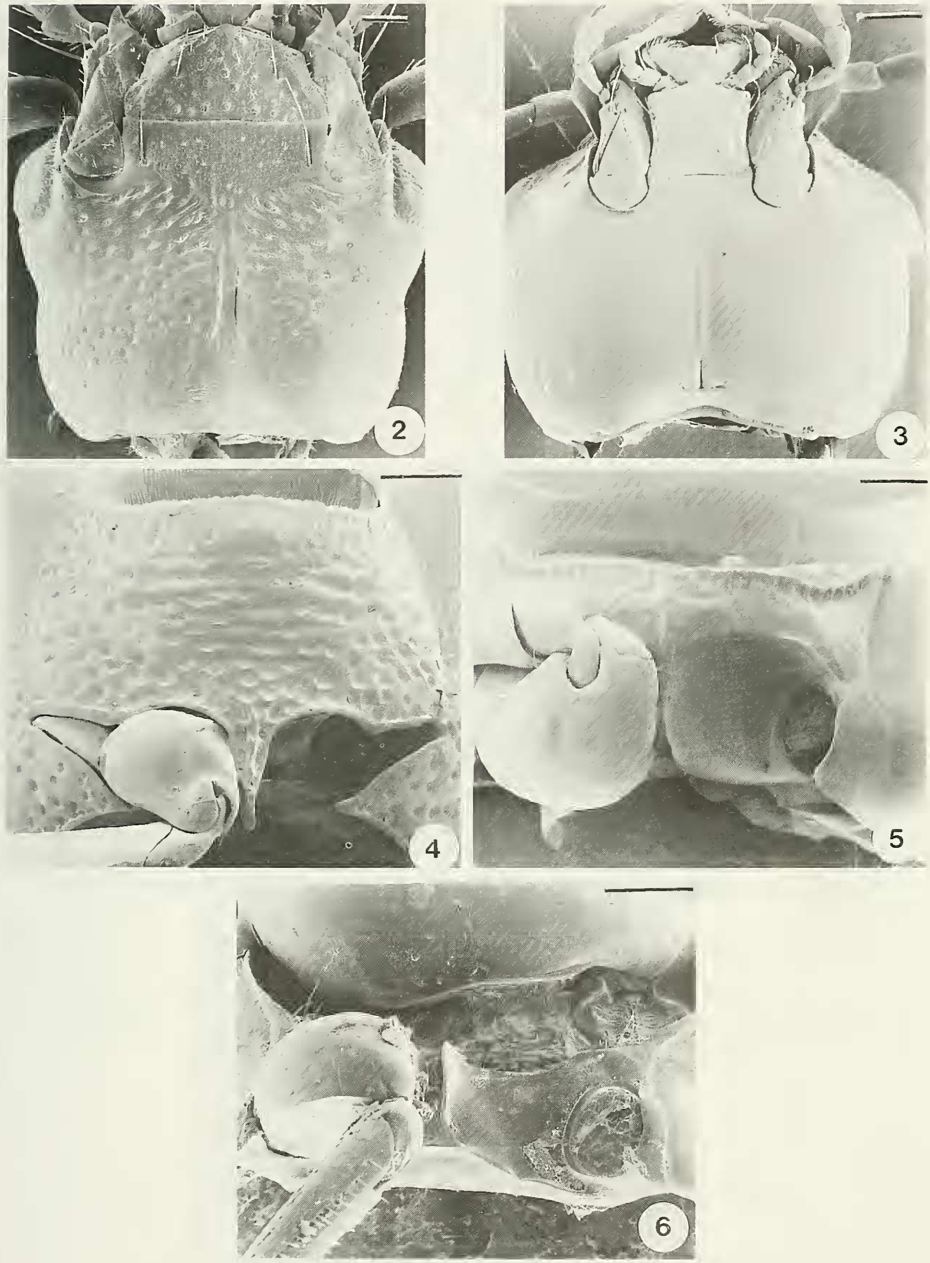
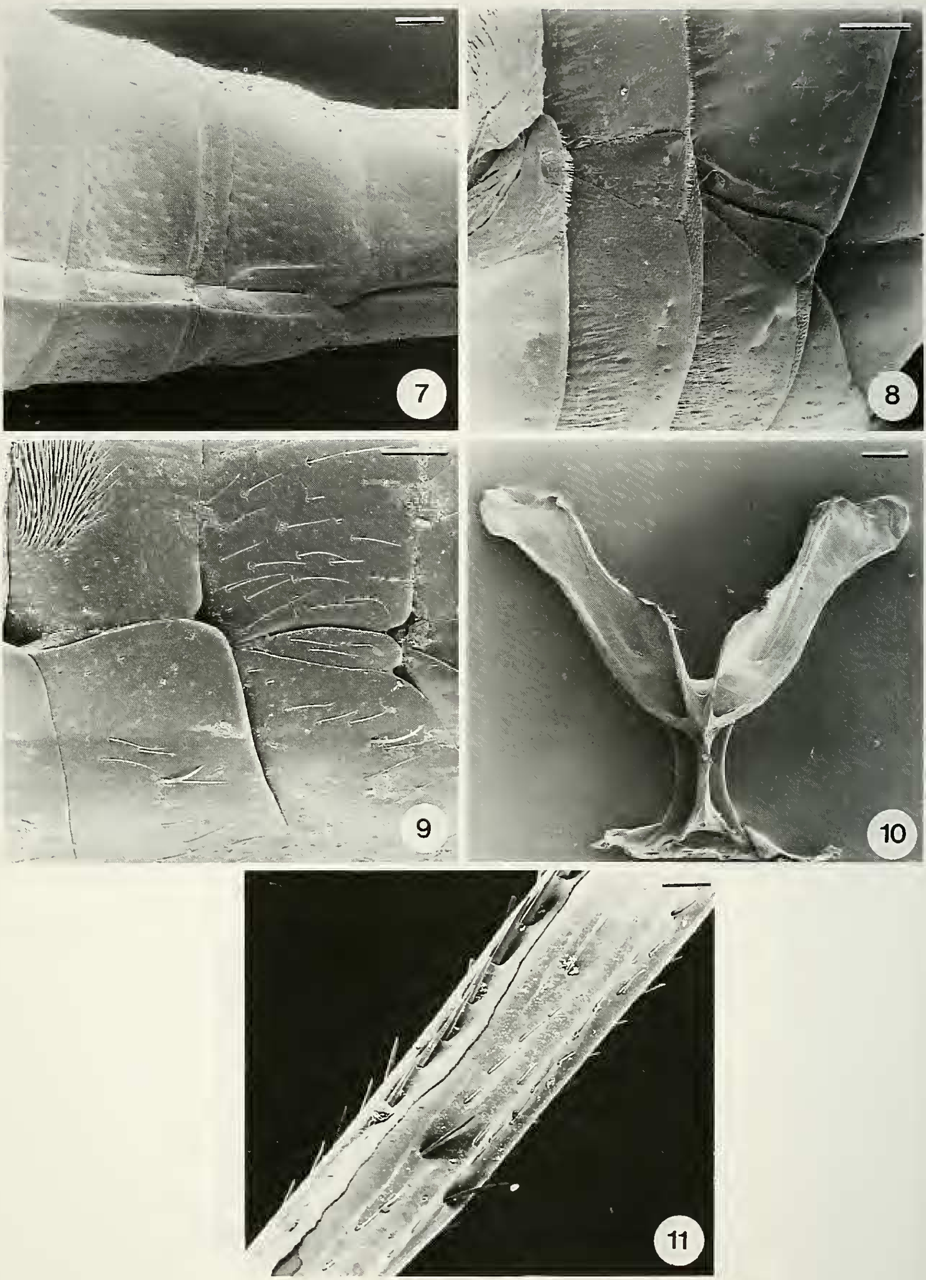


FIG. 1a

Habitus of *Euscaphidium tuberosum*, lateral and dorsal views.

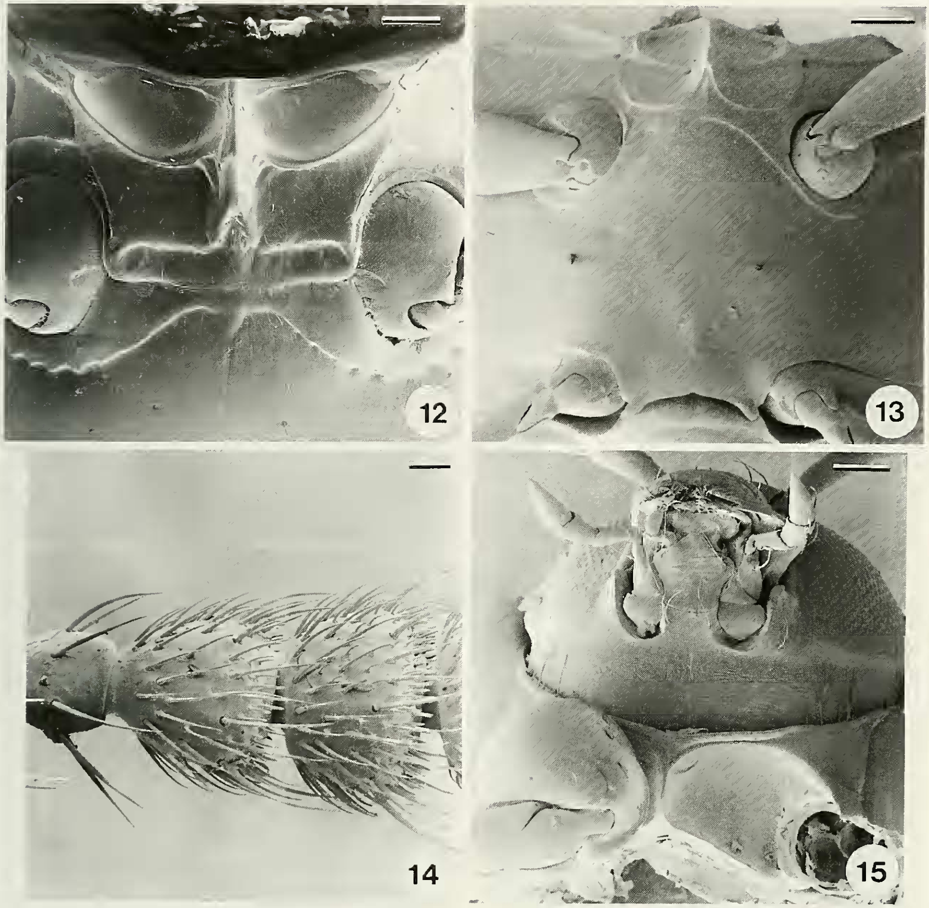


FIGS 2-6
2, *Trigonurus asiaticus*, head, ventral view (scale bar 100 µm); 3, *Scaphidium quadrimaculatum*, head, ventral view (scale bar 200 µm); 4, *Trigonurus asiaticus*, prosternum (scale bar 200 µm); 5, *Scaphidium quadrimaculatum*, prosternum (scale bar 200 µm); 6, *Scaphisoma agaricinum*, prosternum (scale bar 100 µm).



FIGS 7-11

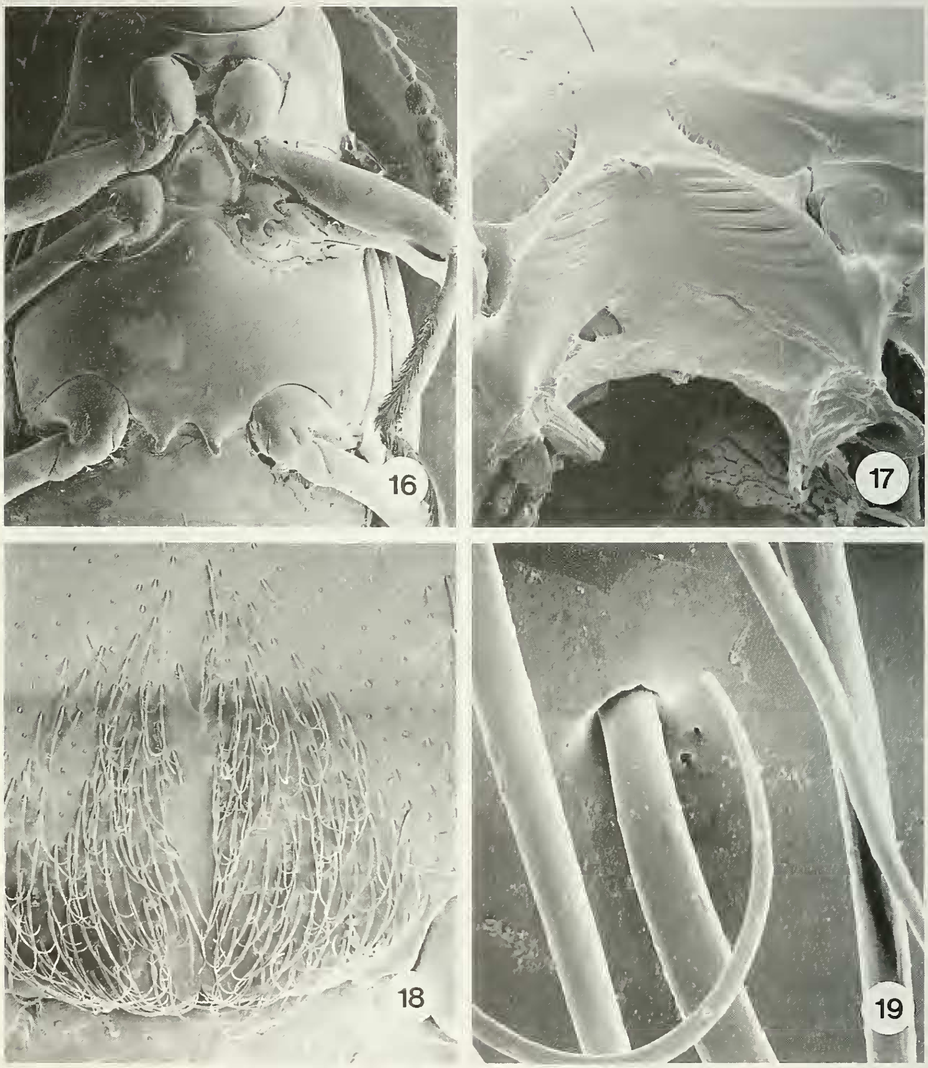
7, *Trigonurus asiaticus*, paratergites (scale bar 100 µm); 8, *Scaphidium quadrimaculatum*, paratergites (scale bar 100 µm); 9, *Scaphisoma agaricinum*, paratergites (scale bar 50 µm); 10, *Scaphidium quadrimaculatum*, metendosternite (scale bar 200 µm); 11, same, portion of metatibia (scale bar 50 µm).



FIGS 12-15
12, *Scaphidium quadrimaculatum*, ventral view of mesonotum; 13, *Cyparium terminale*, ventral view of body; 14, same, ventral view of antenna; 15, same, head and prothorax, ventral view.

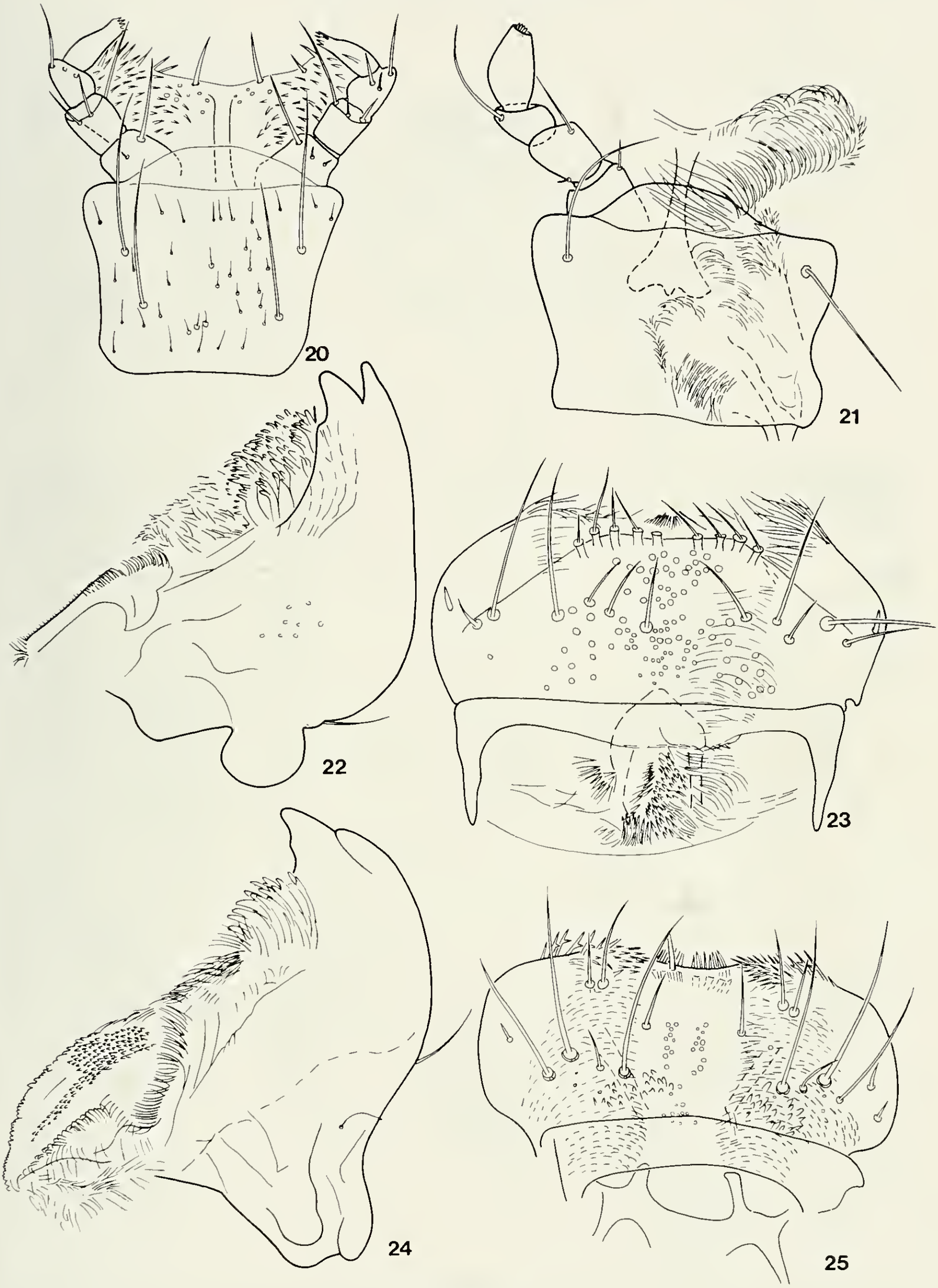
ACKNOWLEDGMENTS

We thank Nicolle Berti, Muséum National d'Histoire Naturelle, Paris, for the loan of the type specimen of *Cerambyciscapha dohertyi*, Roberto Poggi, Museo Civico di Storia Naturali, Genova, for the loan of the type of *Euscaphidium tuberosum*, and Malcolm Kerley, The Natural History Museum, London, for the type of *Kathetopodion borneense*. Additional material for study was kindly supplied by David Kistner, Alfred F. Newton, Shun-Ichiro Naomi, and Steve Ashe. Shun-Ichiro Naomi and Takehiko Nakane provided us with valuable biological information on Japanese species. Scanning electron micrographs were made with the assistance of Bruce Cutler and Jean



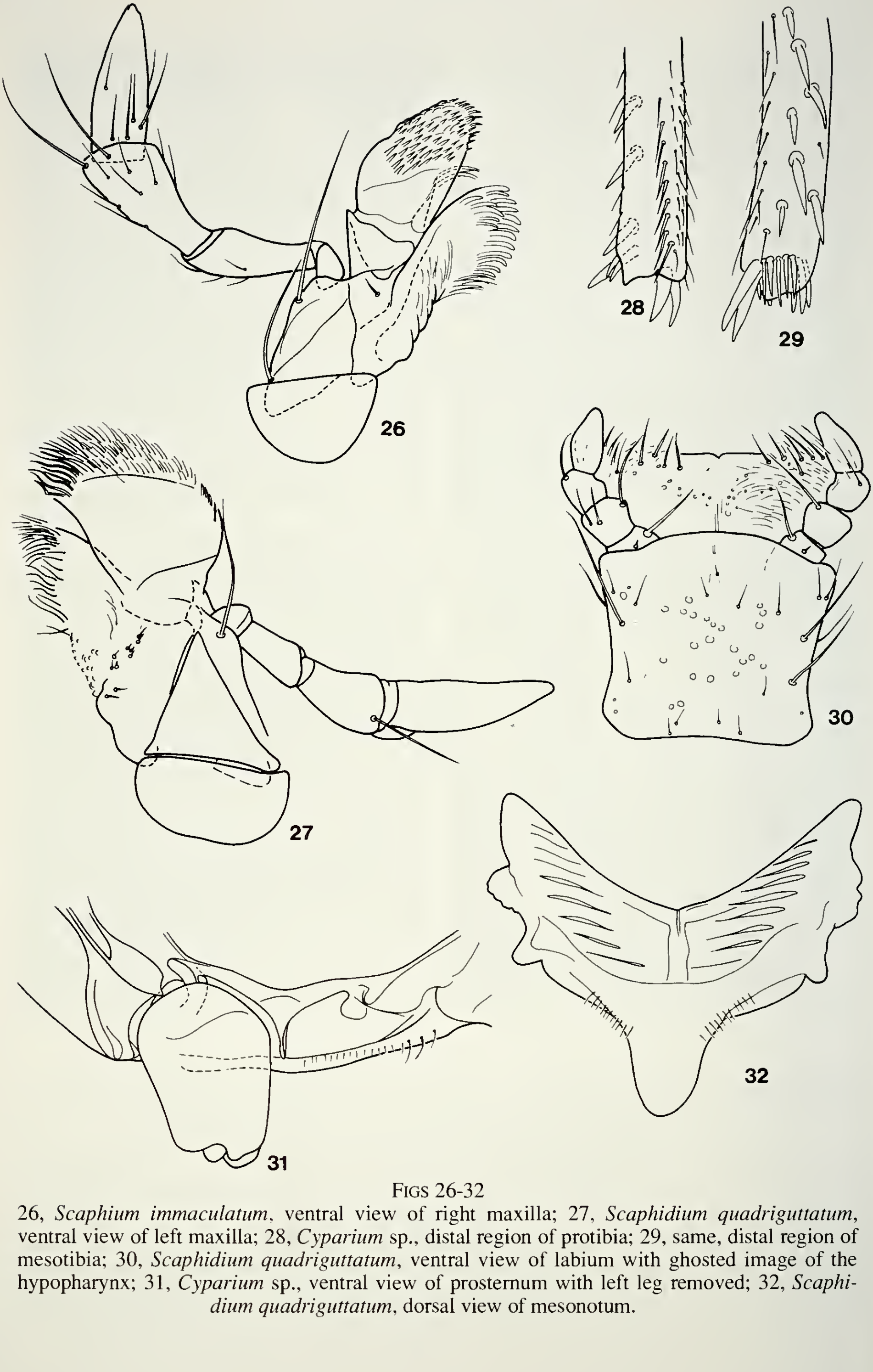
Figs 16-19
16, *Scaphium immaculatum*, ventral view of male; 17, *Scaphidium qadrimaculatum*, anterior view of mesonotum showing prescutal files of male; 18, same, ventral view of setal patch of male 19, same, close-up image of the base of a seta part of the male setal patch.

Wüest. The habitus illustration of *D. wallacei* was drawn by Steve Lingafelter. The illustrations of *E. tuberosum* were drawn by Nicolette Lavoyer. This study would not have been accomplished without a two visiting grants to RABL from the Muséum d'histoire naturelle, Geneva. We gratefully appreciate review of this paper by Steve Ashe, and comments by A. F. Newton, Jr. and Daniel Burckhardt.



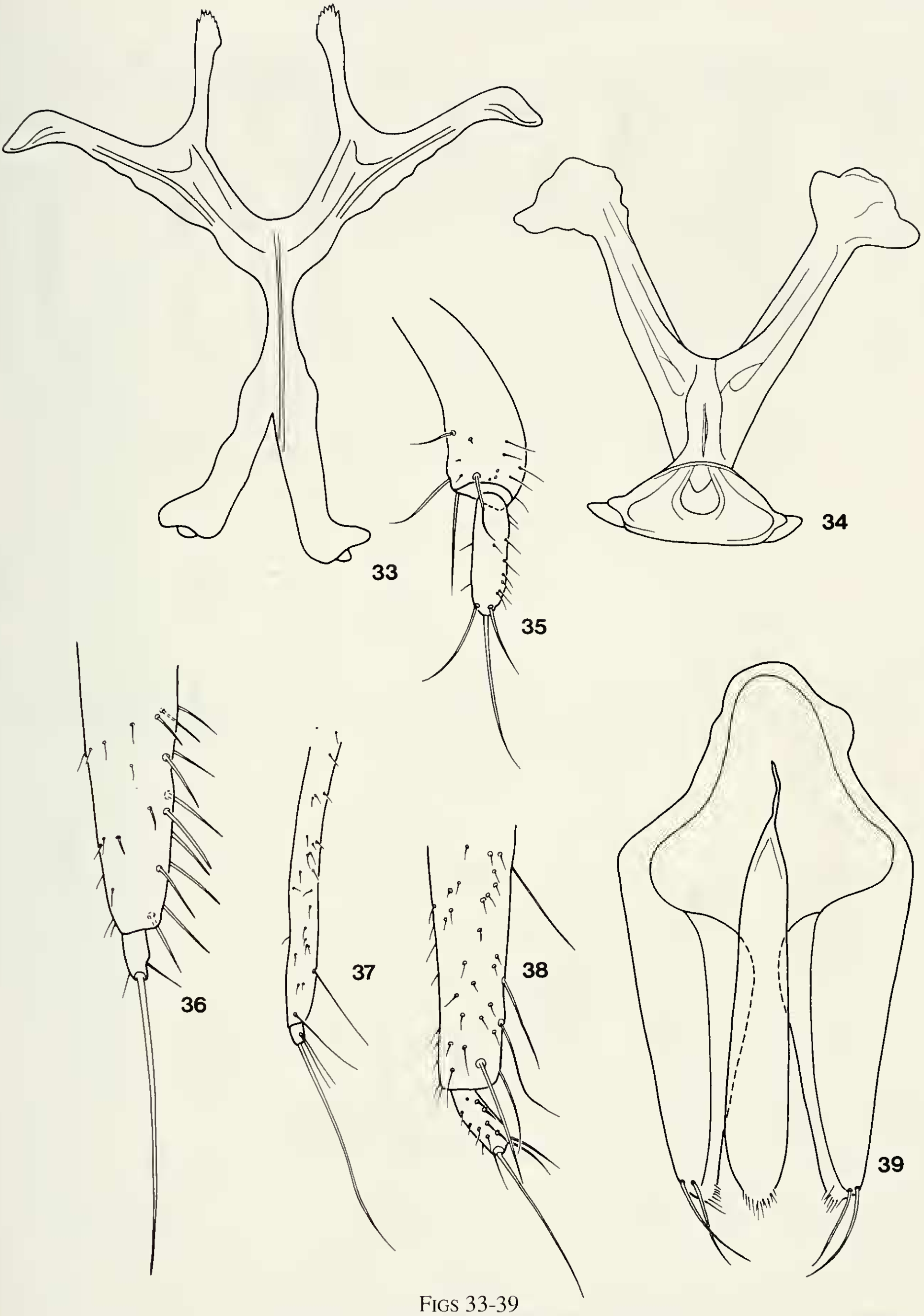
FIGS 20-25

20, Labium of *Cerambyciscapha dohertyi*, ventral view with ghosted image of hypopharynx; 21, *Scaphium immaculatum*, ventral view with ghosted image of hypopharynx; 22, *Scaphidium quadriguttatum*, ventral view of left mandible; 23, *Scaphium immaculatum*, dorsal view of clypeus with ghosted image of epipharynx; 24, same ventral view of left mandible; 25, *Cerambyciscapha dohertyi*, dorsal view of clypeus with ghosted image of epipharynx.



FIGS 26-32

26, *Scaphium immaculatum*, ventral view of right maxilla; 27, *Scaphidium quadriguttatum*, ventral view of left maxilla; 28, *Cyparium* sp., distal region of protibia; 29, same, distal region of mesotibia; 30, *Scaphidium quadriguttatum*, ventral view of labium with ghosted image of the hypopharynx; 31, *Cyparium* sp., ventral view of prosternum with left leg removed; 32, *Scaphidium quadriguttatum*, dorsal view of mesonotum.



Figs 33-39

33, *Trigonurus asiaticus*, anterior view of metendosternite; 34, *Scaphium castanipes*, anterior view of metendosternite (anterior tendons not shown); 35, *Cyparium* sp., coxite of female; 36, *Nodynus japonicus*, coxite of female; 37, *Pseudobironium lewisi*, coxite of female; 38, *Episcaphium saucineum*, coxite of female; 39, *Cerambyciscapha dohertyi*, ventral view of male abdominal sternites 8 and 9.

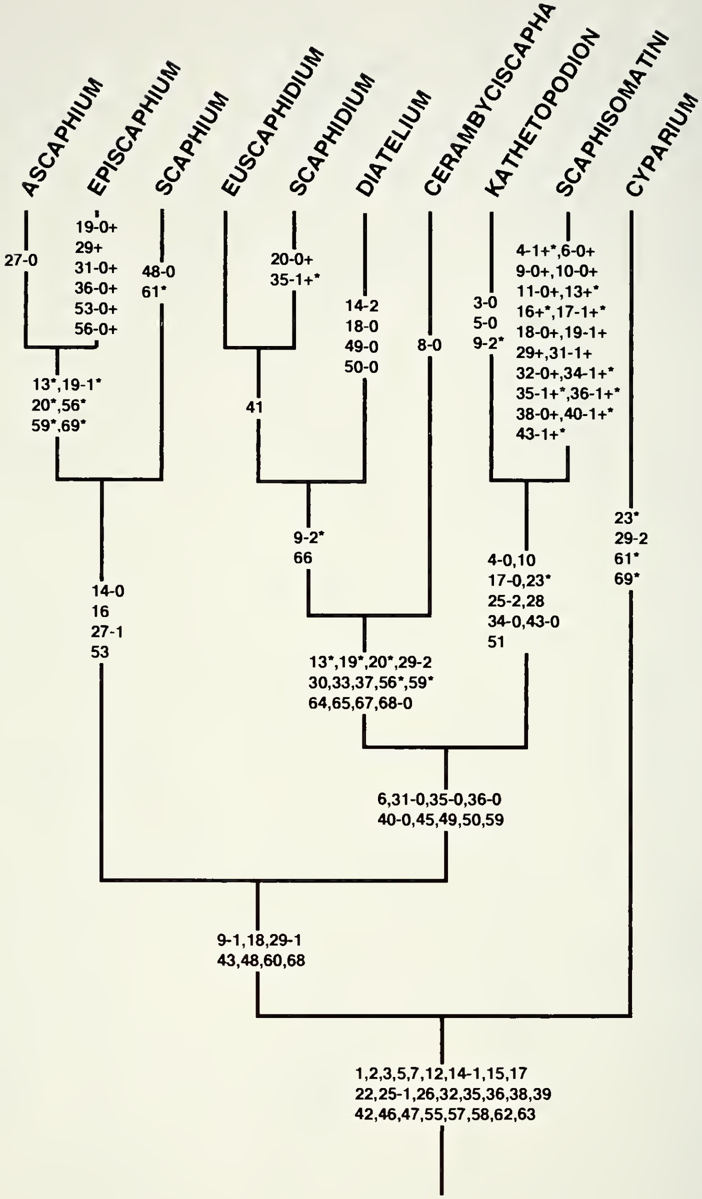


Fig. 40

Cladogram showing the relationships among members of Scaphidiinae. This cladogram was produced by a cladistic analysis using a generalized outgroup to polarize characters. Characters 21, 24, 44, 52, and 54 are uninformative in this analysis and are not mapped onto the cladogram. Homoplasy = *, Polymorphism = +

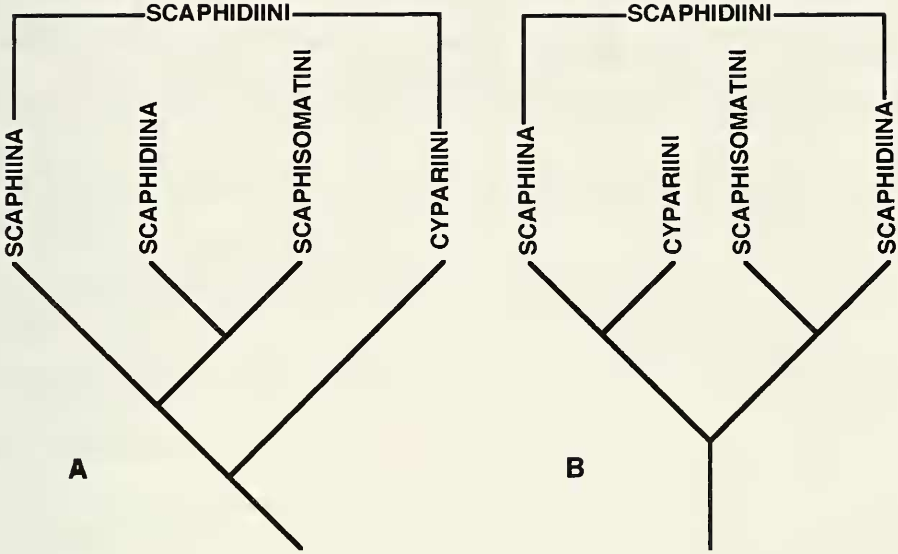


FIG. 41
Two cladograms showing the relationships among members of the higher taxa of Scaphidiinae. Note that Scaphidiini are paraphyletic with respect to the phylogenetic placement of the other tribes.

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APPENDIX: CATALOGUE OF THE CYPARIINI, SCAPHIINI AND SCAPHIDIINI

The list below includes all known published specific and infraspecific names, junior homonyms excepted. Species we have examined for the phylogenetic analysis are indicated by the following signs preceeding the name; (+), dissected species; (-), external and aedeagal characters checked.

Cypariini

Cyparium

anale Reitter, 1880	Neotropical
ater Casey, 1900	Nearctic
basilewskyi Pic, 1955	Africa
bowringi Achard, 1922	SE Asia
championi Matthews, 1888	Neotropical
collare Pic, 1920	Neotropical
+*concolor* (Fabricius, 1801)	Nearctic
flavipes LeConte, 1860	
substriatum Reitter, 1880	
ferrugineum Pic, 1920	Neotropical
flavosignatum Zayas, 1989	Neotropical
ssp *bicolorum* Zayas, 1989	
ssp *funebre* Zayas, 1989	
ssp *splendidum* Zayas, 1989	
formosanum Miwa & Mitono, 1943	SE Asia
grilloi Pic, 1920	Neotropical
grouvellei Pic, 1920	Neotropical
humerale Achard, 1922	Neotropical
inclinans Kirsch, 1873	Neotropical
-*javanum* Löbl, 1990	SE Asia
khasianum Löbl, 1984	SE Asia
-*laevisternale* Nakane, 1956	E Palaearctic
mathami R. Oberthür, 1884	Neotropical
-*mikado* Achard, 1923	E Palaearctic
minutum Pic, 1931	Neotropical
-*montanum* Achard, 1922	SE Asia

monticola Miwa & Mitono, 1943	SE Asia
multistriatum Pic, 1954	Africa
nigronotatum Pic, 1931	Neotropical
oberthueri Pic, 1955	Neotropical
palliatum Erichson, 1845	Neotropical
pallidum Pic, 1955	Africa
peruvianum Pic, 1947	Neotropical
piceum Reitter, 1880	S Africa
plagipenne Achard, 1922	SE Asia
punctatum Pic, 1916	SE Asia
pygidiale Achard,1922	Neotropical
ruficolle Achard, 1922	Neotropical
rufohumerale Pic, 1931	Neotropical
rufonotatum Pic, 1916	Neotropical
sallei Matthews, 1888	Neotropical
semirufum Pic, 1917	SE Asia
siamense Löbl, 1990	SE Asia
-*sibiricum* Solsky, 1871	E Palaearctic
submetallicum Reitter, 1880	? SE Asia
tamil Löbl, 1979	SE Asia
+*terminale* Matthews, 1888	Neotropical
tenenbaumi Pic, 1926	E Palaearctic
testaceicorne Pic, 1931	Neotropical
testaceum Pic, 1920	SE Asia
variabile Pic, 1955	Africa
var. *atrocinctum* Pic, 1955	
var. *diversipenne* Pic, 1955	
variegatum Achard, 1920	SE Asia
-*yunnanum* (Achard, 1920)	SE Asia

Scaphiini

Ascaphium

-*apicale* Lewis, 1893	E Palaearctic
-*minor* Pic, 1954	SE Asia
-*ochripes* Löbl, 1992	SE Asia
-*sinense* Pic, 1954	SE Asia
-*sulcipenne* Lewis, 1893	E Palaearctic
+*tibiale* Lewis, 1893	E Palaearctic
tonkinense Achard, 1921	SE Asia

Episcaphium

*tranferred from *Phenoscaphium*

-*callosipenne* (Achard, 1922), **comb.nov.***	SE Asia
+*saucineum* (Motschulsky, 1859)	SE Asia
-*semirufum* Lewis, 1893	E Palaearctic
var. *ruficolle* Lewis, 1893	
-*unicolor* Löbl, 1992	SE Asia

Scaphium

+*castanipes* Kirby, 1837	Nearctic
ferrugineum Reitter, 1880	? S Africa
+*immaculatum* (Olivier, 1790)	W Palaearctic
rufipes Reitter, 1883	
-*quadraticolle* Solsky, 1874	C Asia

Scaphidiini

Euscaphidium

-*tuberosum* Achard, 1922	SE Asia

Scaphidium

* = transferred from *Scaphidiolum*
** = transferred from *Hemiscaphium*
***=transferred from *Ascaphidium*
+ = transferred from *Scaphidiopsis*
++ = transferred from *Falsoascaphidium*
+++ = transferred from *Cribroscaphium*

abdominale Achard, 1920	SE Asia
abyssinicum (Pic,,1954), **comb.nov.***	Africa
alpicola Blackburn, 1891	Australia
alpicolum ; Löbl, 1976 (incorr. subsequent spelling)	
alternans Löbl, 1978	New Guinea
amurense Solsky,1871	E Palaearctic
ab. *bodemeyeri* Reitter, 1913	
andrewesi Achard, 1922)	SE Asia
var. *femoratum* Achard, 1922	
angolense Pic, 1940	Africa
angustatum Pic, 1920	Madagascar
antennatum Reitter, 1880	Nearctic
anthrax Achard, 1920	SE Asia
apicicorne (Pic,1953), **comb.nov.***	Madagascar
-*arrowi* Achard, 1920	SE Asia
aterrimum Reitter, 1880	SE Asia
atricolor Pic, 1915	SE Asia
atripenne Gestro, 1879	SE Asia
atripes Pic 1946	Africa
atrosuturale Pic, 1915	SE Asia
atrum Matthews, 1888	Neotropical
baconi Pic, 1915	SE Asia
var. *assamense* Pic, 1915	
var. *multimaculatum* Pic, 1915	
var. *semifasciatum* Pic, 1915	
var. *uniplagatum* Achard, 1922	
badium Heller, 1917	SE Asia
+*basale* Castelnau, 1940, **comb.nov.***	Madagascar
basilewskyi (Pic, 1955), **comb.nov.***	Africa
benitense (Achard, 1922), **comb.nov.***	Africa
bicinctum Achard, 1920	SE Asia
anamalaiense Löbl, 1971	
nathani Löbl, 1971	
bicolor Castelnau, 1840	Madagascar
var. *unicolor* Castelnau, 1840	
bifasciatum Pic, 1915	SE Asia
bilineatithorax (Pic, 1931), **comb.nov.***	SE Asia
binhanum (Pic, 1925), **comb.nov.***	SE Asia
binigronotatum (Pic, 1931), **comb.nov.***	Africa
binominatum Achard, 1915	SE Asia
binotatum Achard 1915	SE Asia
bipunctatum Redtenbacher, 1867	Neotropical
bisbimaculatum Pic, 1917	Neotropical
biseriatum Champion, 1927	SE Asia

biundulatum Champion, 1927	SE Asia
bolivianum (Pic, 1931), **comb.nov.**	Neotropical
borneense Pic, 1915, **comb.nov.****	SE Asia
-*brunneopictum* (Achard, 1922), **comb.nov.****	SE Asia
carinense Achard, 1920	SE Asia
castaneicolor Csiki, 1924	SE Asia
castaneum Perty, 1830	Neotropical
celebense Pic, 1915	SE Asia
cerasinum R. Oberthür, 1884	Neotropical
+*chapuisi* Gestro, 1880	SE Asia
cheesmanae Löbl, 1975	New Guinea
chinense Li, 1992	SE Asia
-*chujoi* Löbl, 1967	E Palaearctic
cinnamoneum Champion, 1927	SE Asia
clathratum Achard, 1920	SE Asia
coerulans Löbl, 1979	New Guinea
comes Löbl, 1968	E Palaearctic
compressum Achard, 1915	SE Asia
confusum (Pic, 1926), **comb.nov.***	SE Asia
conjunctum Motschulsky, 1859	SE Asia
consimile Achard, 1920	SE Asia
consobrinum Castelnau, 1840	Madagascar
-*coomani* (Pic, 1925)	SE Asia
coronatum Reitter, 1880	Australia
cyanellum R. Oberthür, 1884	SE Asia
cyanipenne Gestro, 1879	New Guinea
decorsei Achard, 1920	Madagascar
delatouchei Achard, 1920	SE Asia
deletum Heer, 1847 (fossil)	Tertiary, Oeningen
discerptum (Achard, 1922), **comb.nov.****	SE Asia
disclusum (Achard, 1924), **comb.nov.***	SE Asia
discoidale Pic, 1920	Madagascar
discomaculatum (Pic, 1954), **comb. nov.***	Africa
disconotatum Pic, 1915	SE Asia
distinctum Achard, 1916	Australia
dohertyi Pic, 1915, **comb.nov.****	SE Asia
donckieri Pic, 1917	Madagascar
dureli (Achard, 1922)	SE Asia
egregium Achard, 1922	SE Asia
elisabethae (Pic, 1954), **comb.nov.***	Africa
ellenbergeri (Paulian, 1951), **comb.nov.***	Africa
elongatum Achard, 1915	SE Asia
emarginatum Lewis, 1893	E Palaearctic
exclamans R. Oberthür, 1884	Neotropical
exornatum R. Oberthür, 1884	Australia
australe Achard, 1916	
fainanense Pic, 1915	SE Asia
fairmairei Pic, 1920	Madagascar
fasciatomaculatum R. Oberthür, 1884	Neotropical
fasciatum Castelnau, 1840	Madagascar
fascipenne Reitter, 1880	Neotropical
feai Pic, 1920	SE Asia
femorale Lewis, 1893	E Palaearctic
flavofasciatum Champion, 1913	Neotropical
flavomaculatum Miwa & Mitono, 1943	SE Asia

formosanum Pic, 1915	SE Asia
fossulatum Pic, 1921	SE Asia
fraternum Achard, 1920	SE Asia
fryi Achard, 1920	SE Asia
fukienense Pic, 1954	SE Asia
gabonicum (Paulian, 1951), **comb.nov.***	Africa
geniculatum R. Oberthür, 1884	Neotropical
gestroi Pic, 1920	SE Asia
gibbosum Pic, 1915	SE Asia
gounellei Pic, 1920	Neotropical
gracile Achard, 1920	SE Asia
-*grande* Gestro, 1880	SE Asia
inimpressum Pic, 1920	
subannulatum Pic, 1915	
var. *melanopus* Achard, 1924	
grandidieri Achard, 1920	Madagascar
grouvellei Achard, 1920	SE Asia
gurung Löbl, 1992	SE Asia
hageni Weyenbergh (fossil)	Jurassic, Solenhofen
harmandi Achard, 1920	SE Asia
-*hexaspilotum* (Achard, 1924)	SE Asia
holzschuhi Löbl, 1992	SE Asia
ifanense (Pic, 1947), **comb.nov.***	Africa
impictum Boheman, 1851	S Africa
impuncticolle Pic, 1915, **comb.nov.****	SE Asia
incisum Lewis, 1893	E Palaearctic
incrassatum Achard, 1920	SE Asia
indicum Löbl, 1979	SE Asia
innotatum (Pic, 1940), **comb.nov.***	SE Asia
inornatum Gestro, 1880	SE Asia
interruptum Fairmaire, 1897	Madagascar
irregulare Pic, 1920, **comb.nov.+++**	SE Asia
-*jacobsoni* Achard, 1921	SE Asia
japonum Reitter, 1877	E Palaearctic
japonicum ; Lewis, 1893 (incorr. subsequent spelling)	
longipes Lewis, 1891	
javanum Pic, 1915	SE Asia
klapperichi Pic, 1954	SE Asia
lafertei Pic, 1920	Madagascar
laosense (Pic, 1928), **comb.nov.***	SE Asia
lateflavum (Pic, 1928), **comb.nov.***	SE Asia
latissimum Achard, 1915	Madagascar
leleupi (Pic, 1954), **comb.nov.***	Africa
var. *atropygum* Pic, 1954	
lesnei Achard, 1920	SE Asia
lewisi (Achard, 1923), **comb.nov.***	E Palaearctic
lineaticolle Matthews, 1888	Neotropical
lineatipes (Pic, 1925), **comb.nov.***	Africa
longicolle Pic, 1915	SE Asia
var. *bicoloripes* Pic, 1948	
var. *kudatense* Pic, 1948	
longipenne Achard, 1921	SE Asia
longithorax Pic, 1916	SE Asia
var. *nigriventre* Achard, 1924	
lucidum Achard, 1915	Neotropical

lunatum Motschulsky, 1859	SE Asia
lunulatum ; Pic, 1921 (incorr.subsequent spelling)	
var. *bioculatum* Achard, 1924	
var. *inconjunctum* Pic, 1921	
var. *rufithorax* Pic, 1921	
luteomaculatum (Pic, 1923), **comb.nov.***	SE Asia
luzonicum (Achard, 1924), **comb.nov.***	SE Asia
maculaticeps (Pic, 1923), **comb.nov.***	SE Asia
madecassum Pic, 1917	Madagascar
madurense Achard, 1915	SE Asia
malaccanum Pic, 1915	SE Asia
mangenoti (Paulian, 1951), **comb.nov.***	Africa
marginale Reitter 1880	SE Asia
marginatum Matthews, 1888	Neotropical
martapuranum Pic, 1916	SE Asia
mastersi Macleay, 1871	Australia
matthewsi Csiki, 1904	Neotropical
mayneui (Pic, 1954), **comb.nov.***	Africa
medionigrum Pic, 1915	SE Asia
melanogaster Löbl, 1992	SE Asia
melli Löbl, 1972	SE Asia
metallescens Gestro, 1879	New Guinea
mexicanum Castelnau, 1840	Neotropical
minutum Pic, 1920	SE Asia
monteithi Löbl, 1976	Australia
montivagum Shirôzu & Morimoto, 1963	E Palaearctic
morimotoi Löbl, 1982	E Palaearctic
takashii Shirôzu & Morimoto, 1963	
multinotatum Pic, 1921	SE Asia
multipunctatum (Pic, 1928), **comb.nov.***	Africa
var. *luluanum* Pic, 1954	
negrito Heller, 1917	SE Asia
nepalense Löbl, 1992	SE Asia
nigripes Chevrolat, 1830	Neotropical
nigrocinctulum R. Oberthür, 1884	SE Asia
nigromaculatum Reitter, 1880	SE Asia
var. *effigiatum* Achard, 1922	
nigrosuturale Pic, 1920	SE Asia
nigrum Castelnau, 1840	Madagascar
notaticolle Pic, 1915	SE Asia
notatum (Pic, 1923)	Australia
ocellatum Achard, 1920	SE Asia
var. *birmanica* [sic] Achard, 1920	
oculare (Pic, 1923), **comb.nov.***	Madagascar
optabile (Lewis, 1893)	E Palaearctic
orbiculosum Reitter, 1880	SE Asia
ornatum Casey, 1900	Nearctic
overlaeti (Pic, 1954), **comb.nov.***	Africa
palonense Achard, 1920	SE Asia
pantherinum R. Oberthür, 1883	Neotropical
papuanum Löbl, 1975	New Guinea
+*pardale* Castelnau, 1840	Neotropical
var. *nigripenne* R. Oberthür, 1884	
patinoi R. Oberthür, 1884	Neotropical
pauliani **nom. nov.** for *sulcatum* Paulian, 1941 (secondary junior homonym of *S. sulcatum* (Pic, 1915))	Africa

peninsulare Achard, 1920, **comb.nov.****	SE Asia
peraffine R. Oberthür, 1884	Neotropical
-*perpulchrum* Csiki, 1909	SE Asia
philippense Reitter, 1880	SE Asia
phungi Pic, 1923	SE Asia
picconii Gestro, 1880	SE Asia
var. *sexmaculatum* Reitter, 1889	
piceoapicale (Pic, 1940), **comb.nov.***	SE Asia
plagatum Achard, 1920	SE Asia
politum Fairmaire, 1899	Madagascar
prolongatum (Pic, 1928), **comb.nov.***	Africa
pulchellum Reitter, 1880	Madagascar
punctaticolle Pic, 1923	SE Asia
punctatum Castelnau, 1840	Madagascar
punctipenne Macleay, 1871	Australia
coronatum Reitter, 1880	
thoracicum Achard, 1916	
pygidiale Pic, 1917	Madagascar
var. *bicoloricolle* Pic, 1917	
+*quadriguttatum* Say, 1823	Nearctic
amplum Casey, 1900	
piceum Melsheimer, 1846	
obliteratum LeConte, 1860	
quadrinotatum Castelnau, 1840	
quadripustulatum Say, 1823	
quadrillum Fairmaire, 1898	Madagascar
var. *biconjuntum* Pic, 1920	
-*quadrimaculatum* Olivier, 1790	W Palaearctic
quadriplagatum Achard, 1915	SE Asia
quadriplagiatum ; Pic, 1916 (incorr.subsequent spelling)	
quadripustulatum (Fabricius, 1775)	Australia
bimaculatum Macleay, 1871	
quinquemaculatum Pic, 1915	Neotropical
reductum (Pic, 1954), **comb.nov.***	Africa
reitteri Lewis, 1879	E Palaearctic
insulare Achard, 1922	
rosenbergi Pic, 1955	Neotropical
rouyeri Pic, 1915	SE Asia
rubicundum Reitter, 1879	Neotropical
rubricolle (Pic, 1951), **comb.nov.***	Madagascar
rubritarse Pic, 1915	SE Asia
ruficolor Pic, 1915	SE Asia
ruficorne Fairmaire, 1898	Madagascar
rufipenne Pic, 1917	Madagascar
rufipes Pic, 1922	SE Asia
rufitarse Achard, 1920	SE Asia
var. *modigliani* Pic, 1920	
rufofemoratum Pic, 1921	SE Asia
rufonotatum (Pic, 1928), **comb.nov.***	SE Asia
rufopygum Lewis, 1893	E Palaearctic
rufum Brancsik, 1893	Madagascar
-*rugatum* Löbl, 1976	New Guinea
salvazai (Pic, 1928), **comb.nov.***	SE Asia
sauteri Miwa & Mitono 1943	SE Asia
semiflavum Gestro, 1880	SE Asia

semilimbatum Pic, 1917	SE Asia
septemmaculatum (Pic, 1940), **comb.nov.***	SE Asia
septemnotatum Champion, 1927	SE Asia
seriatum Heller, 1917	SE Asia
shelfordi (Achard, 1922), **comb.nov.****	SE Asia
shirakii Miwa & Mitono, 1943	SE Asia
shibatai Kimura, 1987	SE Asia
+*sikorai* (Pic, 1915), **comb.nov.*****	Madagascar
simile Castelnau, 1840	Madagascar
simplicicolle (Pic, 1923), **comb.nov.****	SE Asia
sinense Pic, 1954	SE Asia
sinuatum Csiki, 1924	SE Asia
sondaicum Gestro, 1880	SE Asia
striatipenne Gestro, 1880, **comb.nov.****	SE Asia
striatum Pic, 1920	SE Asia
suarezicum Pic, 1920	Madagascar
subdepressum Pic, 1921, **comb.nov.++**	SE Asia
subelongatum Pic, 1915	SE Asia
subpunctatum (Pic, 1951), **comb.nov.***	Madagascar
sulcaticolle (Pic, 1923), **comb.nov.****	SE Asia
sulcatum (Pic, 1915), **comb.nov.****	SE Asia
sulcipenne Gestro, 1880, **comb.nov.****	SE Asia
sylhetense Achard, 1920	SE Asia
takahashii Miwa & Mitono, 1943	SE Asia
takemurai Nakane, 1956	E Palaearctic
testaceum Reitter, 1880	Neotropical
thakali Löbl, 1992	SE Asia
thomasi (Pic, 1926), **comb.nov.***	SE Asia
transversale Matthews, 1888	Neotropical
tricolor Achard 1920, **comb.nov.****	SE Asia
trimaculatum Löbl, 1976	Australia
trinotatum Pic, 1920	SE Asia
tsushimense Shirôzu & Morimoto, 1963	E Palaearctic
tuberculipes (Löbl, 1972), **comb.nov.***	SE Asia
undulatum Pic, 1915	Neotropical
unifasciatum Pic, 1916	SE Asia
vagefasciatum Pic, 1920	Madagascar
variabile Matthews, 1888	Neotropical
variegatum Pic, 1915	Neotropical
var. *portevini* Pic, 1920	
vernicatum (Pic, 1954)	SE Asia
vicinum Pic, 1915	SE Asia
violaceipenne Pic, 1927	SE Asia
viride Löbl, 1978	New Guinea
vitalisi Achard, 1920	SE Asia
vittipenne R. Oberthür, 1884	Neotropical
waterstradti Pic, 1915	SE Asia
yasumatsui Shirôzu & Morimoto, 1963	E Palaearctic
yunnanum Fairmaire, 1886	SE Asia

Cerambyciscapha

-*dohertyi* Pic, 1915	SE Asia

Diatelium

+*wallacei* Pascoe, 1863	SE Asia
spectrum (Vollenhoven, 1865)	
var. *laterale* Achard, 1920	